



Reassessment of multiple species of *Gymnelus* (Teleostei: Zoarcidae) in Pacific Arctic and boreal regions

CATHERINE W. MECKLENBURG^{1,2,4} & M. ERIC ANDERSON³

¹California Academy of Sciences, 55 Music Concourse Drive, San Francisco, California 94118 USA

²Point Stephens Research, P.O. Box 210307, Auke Bay, Alaska 99821 USA

³South African Institute for Aquatic Biodiversity, Private Bag 1015, Grahamstown 6139, South Africa

⁴Corresponding author. E-mail: ptstephens@alaskan.com

Abstract

Recently described new nominal species and resurrected species in the eelpout genus *Gymnelus* Reinhardt 1834 were re-assessed for validity using fresh material collected in Pacific Arctic regions and a large body of data from a previous systematic review of the genus. The analysis reported here included both DNA barcodes and morphology. Only two species were validated: *G. viridis* (Fabricius 1780) and *G. hemifasciatus* Andriashev 1937. The latter species occurred as two morphotypes for which there is some evidence of difference in ecological preference, but the available environmental data are not robust enough to firmly identify or verify ecophenotypes.

Key words: Zoarcidae, *Gymnelus*, eelpouts, *Gymnelus hemifasciatus*, *Gymnelus viridis*, Arctic, boreal Pacific, DNA barcoding, ecophenotype

Introduction

Species of the eelpout genus *Gymnelus* Reinhardt 1834 are found on the sea floor in shallow Arctic and boreal marine waters. In a systematic review of *Gymnelus* material Anderson (1982) confirmed the validity of four species (*G. hemifasciatus* Andriashev 1937, *G. popovi* [Taranetz & Andriashev 1935], *G. retrodorsalis* Le Danois 1913, and *G. viridis* [Fabricius 1780]) and described one new species (*G. pauciporus* Anderson 1982), for a total of five in the genus. Subsequently Chernova (1998a) redescribed *G. viridis* and resurrected a synonym, *G. bilabrus* Andriashev 1937; revised the descriptions of *G. retrodorsalis* and *G. pauciporus* and described a new species *G. andersoni* (Chernova 1998b); redescribed *G. hemifasciatus* and described a new species *G. knipowitschi* (Chernova 1999a); described four other new *Gymnelus* species from Arctic seas (Chernova 1999b) and four from Far Eastern seas (Okhotsk Sea, northwestern Pacific Ocean, western Bering Sea; Chernova 2000); and suggested a restoration of *G. popovi* to its original genus, *Commandorella* Taranetz & Andriashev 1935 (Chernova 2000). Those actions tripled the number of species in *Gymnelus*, even with removal of *Commandorella*. In Pacific Arctic and boreal regions, some of the new nominal species of *Gymnelus* have been considered phenotypic variants exhibiting morphological plasticity previously known in other eelpouts (mainly polychromatism and variability in cephalic lateralis canals and pores), or ecophenotypes of two widely distributed and recognized species: *G. viridis* (Fabricius 1780) and *G. hemifasciatus* Andriashev 1937 (e.g., Mecklenburg *et al.* 2002; Anderson & Fedorov 2004; Mecklenburg *et al.* 2011).

This paper deals primarily with the two species represented in recent ichthyological and fisheries oceanography investigations in Bering Strait and the East Siberian, Chukchi, and Beaufort seas: the halfbarred pout, *Gymnelus hemifasciatus*, and fish doctor, *G. viridis*. These species have long been familiar to field and laboratory scientists and observers in northern Pacific regions. Accumulation of fresh material for the current analysis began with the first expedition of the Russian–American Long-Term Census of the Arctic (RUSALCA) in 2004, during which Russian and American scientists' identifications of the *Gymnelus* species differed

(Mecklenburg *et al.* 2007). Since then, we have collected material from two more RUSALCA expeditions in 2009 and 2012, and several other expeditions from 2006 to 2013 conducted by other programs; the disagreement over identifications continues. For instance, Chernova (e.g., 2009a, b; pers. comm. 2004–2014) identifies the RUSALCA and other Pacific Arctic material we identify as *G. hemifasciatus* to the new species *G. knipowitschi* Chernova 1999 and *G. platycephalus* Chernova 1999, while relegating the material we identify as *G. viridis* to *Gymnelus* sp. or *G. bilabrus*.

Our observations and data do not support recognition of the new species as being distinct nor the resurrection of *G. bilabrus*. It is important to resolve the taxonomy of these multiple nominal forms because considering them all as distinct species affects assessments of biodiversity by overestimating numbers of species present and, consequently, can give a false idea of the nature of the Arctic fish fauna.

In the fresh samples used in the present analysis, Chernova (2009a,b; pers. comm. 2004–2014) has identified, at different times, *G. barsukovi*, *G. bilabrus*, *G. knipowitschi*, and *G. platycephalus*. In a taxonomic checklist of the Zoarcidae (Anderson & Fedorov 2004), those names were considered to be synonyms of *G. hemifasciatus* and *G. viridis*. We bring recent data from DNA sequencing (barcoding) and morphological examination to resolution of the problem.

In addition to the genetic distances revealed by DNA barcoding, analysis of the fresh sample focuses on coloration and the supratemporal commissure and lateralis pores which Chernova gave as major identifying features for the several nominal forms. For the cephalic lateralis system, the major identifying character specified is whether nominal forms possess a complete or incomplete supratemporal commissure across the back of the head, with usually three (complete commissure) or two (incomplete) lateralis pores. Published accounts indicate that this is a variable character in *Pachycara crossacanthum* (Anderson 1989), *Magadanichthys skopetsi* (Shinohara *et al.* 2004), Greenland to Pacific Arctic *G. viridis* (Anderson 1982), and the nominal *G. andersoni* (Chernova 1998b). Several species of boreal *Lycodes* Reinhardt 1831 exhibit variation in the completeness of lateralis canals, especially the supratemporal, as well (Anderson, unpubl.). In *Bothrocara* Bean 1890 the supratemporal commissure was found to be present, but pore distribution is variable (Anderson *et al.* 2009). In *Lycenchelys scaurus* (Garman 1899) the supratemporal commissure and three pores is typical, but four fish (9.5%) had the commissure complete but lacked pores, two also had the commissure complete but had only the median pore present, and two had the commissure interrupted with only the two lateral pores present (Anderson 1995).

Published accounts also indicate variability in coloration within other eelpout species and coloration is often given as a diagnostic character. *Lycodes marisalbi* Knipowitsch 1906 can be uniformly brown or have white bars (Møller 2000). *Lycodes pallidus* Collett 1879 also has a uniformly brownish morphotype and one with light crossbars (Møller *et al.* 2001). *Lycodes seminudus* Reinhardt 1837 has at least two monochrome morphotypes, including dark gray to almost black and pinkish white (Mecklenburg, unpubl.), as well as a distinctly banded form (Jensen 1904; McAllister *et al.* 1981; Møller & Jørgensen 2000). *Lycodes yamatoi* Toyoshima 1985 has dark and light color forms with the light morphotype exhibiting individually variable banding (Balanov & Kukhlevskii 2011). *Lycodes nakamurae* (Tanaka 1914) also has dark and light color forms with variable intermediate morphotypes (Saveliev *et al.* 2014). *Bothrocara hollandi* (Jordan & Hubbs 1925) has two color forms, a “white” type (pale pinkish) and a “black” type (dark brown or blackish) that are depth-dependent (Okiyama 2004). Chernova also used coloration in the diagnoses of *Gymnelus* species and has described variations within some species, including the nominal forms *G. knipowitschi* (Chernova 1999a) and *G. platycephalus* (Chernova 1999b).

Additional analysis of the data presented by Anderson (1982) completes this reassessment of the nominal species. Since the fresh sample is restricted to material from the Pacific Arctic region, the analyses of nominal species described from the Pacific boreal region, including waters around the western Aleutian Islands and the Pacific Ocean off southeastern Kamchatka, depend primarily on Anderson’s (1982) original data.

Material and methods

The material referred to as the fresh sample includes 221 specimens collected from 2004 to 2013 from the eastern East Siberian Sea, the Chukchi Sea, the western Beaufort Sea, and the northern Bering Sea including Bering Strait. It comprises specimens obtained by the first author during participation in research cruises, specimens provided frozen from other cruises, and specimens from a 2013 survey which were provided from the University of Alaska

Museum. Specimens were photographed and measured for total length (TL) on board, or in the laboratory within a month after receipt of the frozen samples. Some (31, or 14%) specimens had been fixed in formalin before receipt, but all specimens were available less than 9 months after collection while color patterns were still clearly evident and shrinkage from fixation was minimal. Identifications to species were made according to characters given by Anderson (1982), especially color patterns since they were so clear in the fresh material. (In old preserved material with loss of color patterns diagnostic characters include number of pectoral-fin rays, the position of the dorsal-fin origin relative to the pectoral-fin base, and in more difficult cases, numbers of vertebrae.)

The genetic analysis included 67 successfully barcoded specimens (Table 1) from the cruises in 2007 through 2012; barcoding was not an established method at the time of the 2004 cruise, and some of the material from 2012 and 2013 was received already fixed in formalin. In preparation for genetic analysis, the first author removed muscle tissue from the fresh and frozen specimens from the right side well posterior to the anus after wiping the skin clean with an alcohol swab. The specimens were photographed with a barcode sample number label, color strip, and ruler included in each photograph. Lateral views were photographed at a minimum, and many specimens were also photographed in dorsal and ventral view. Notes were taken on coloration for specimens which were not photographed and tissue-sampled.

Tissue samples were placed in 95% ethanol and the whole specimens were fixed in 10% buffered seawater-formalin solution. After fixation specimens were rinsed in water and stored in 70% ethanol before deposition in three museums: California Academy of Sciences, San Francisco (CAS); University of Alaska Museum, Fairbanks (UAM); and the Zoological Institute, Russian Academy of Sciences, St. Petersburg (ZIN).

Tissue samples were sent to the Biodiversity Institute of Ontario, University of Guelph, Canada, for DNA barcoding as contributions to the Fish Barcode of Life initiative. DNA barcoding, which sequences a standard region of the mitochondrial cytochrome *c* oxidase 1 gene (COI), followed the protocol described by Steinke *et al.* (2009a). Sequence data were submitted to the Barcode of Life Data system (BOLD, <http://www.barcodinglife.org>, see Ratnasingham & Hebert [2007]) and to GenBank (accession numbers in Table 1). Specimen and collection data, sequences, specimen images, and trace files are provided in the public dataset “*Gymnelus* GenBank [DS-GYMGBJ]” on BOLD. Neighbor-joining (NJ) analyses and genetic distance calculations were executed with MEGA version 5.0 (Tamura *et al.* 2011). The Kimura 2-parameter (K2P) distance metric (Kimura 1980) was employed for all sequence comparisons and analyses. Confidence in estimated relationships of NJ tree topologies was evaluated by a bootstrap analysis with 1,000 replicates using MEGA version 5.0.

The DNA barcodes were supplemented by morphological observations of the barcoded material as well as numerous other specimens, including some of those studied by Chernova (1998a,b, 1999a,b, 2000, pers. comm.). Specimens of the fresh sample, as well as some from earlier collections, archived in the CAS and UAM were examined together by the authors at the CAS in June 2014. The second author measured standard length (SL), examined the supratemporal commissure for completeness and counted the supratemporal (occipital) and temporal (postorbital) pores (the most variable in eelpouts), and determined sex by observation of the gonads (young) or color of the anal fin (Anderson 1982). We standardized our terminology for the coloration patterns and noted the pattern for each specimen. Notation was taken on whether a depressed fusion of the center of the upper lip was present or absent — a condition in the original diagnosis of *G. bilabrus* (Andriashev 1937) which Anderson (1982) found in only four specimens and Chernova (1998a) found to be absent in a smaller sample.

Original data from Anderson (1982) were also used; see methodology described therein.

Results

DNA sequencing. The DNA barcodes for the 67 *Gymnelus* specimens successfully sequenced place them in two clades: 47 in *G. hemifasciatus* and 20 in *G. viridis* (Fig. 1). The results are similar to those for a somewhat smaller sample reported earlier (Mecklenburg *et al.* 2011). The two clades are clearly separate, yet closely related. The species are separated by only 1.2% sequence divergence (range 0.8–1.9%). There is little intraspecific variation in either clade: 0.4% for *G. hemifasciatus* and 0.1% for *G. viridis*. As can be seen from the NJ tree (Fig. 1), the minor genetic variation seen is not consistent by coloration, sex, or geographic location.

The barcodes from specimens identified as *G. knipowitschi* by Chernova (e.g., CAS 228491, UAM 5520, UAM 5521, ZIN uncatalogued in Table 1) or similar to them (as in, e.g., Mecklenburg *et al.* 2007; Balushkin *et al.* 2011),

including those that could be identified as *G. knipowitschi* from her key (Chernova 2000), fall within the *G. hemifasciatus* clade. In Fig. 1, those are the specimens labeled with an S to indicate the solid-band morphotype (described below). Barcodes from specimens similar to specimens identified by Chernova as *G. platycephalus* (e.g., Mecklenburg *et al.* 2007; Balushkin *et al.* 2011) also fall within the *G. hemifasciatus* clade. In Fig. 1, those are the sequences designated by a T as the typical morphotype. No specimens in our fresh sample could be identified as *G. platycephalus* from the key published in Chernova (2000). The barcodes from specimens similar to *G. bilabrus* and *G. barsukovi* identified by Chernova (e.g., Mecklenburg *et al.* 2007; Balushkin *et al.* 2011) fall within the *G. viridis* clade. We were not able to morphologically distinguish between *G. barsukovi* and *G. bilabrus* in the fresh sample except that the males of *G. viridis* appeared to equate to *G. barsukovi* and the females to *G. bilabrus* (designated by male and female symbols in Fig. 1).

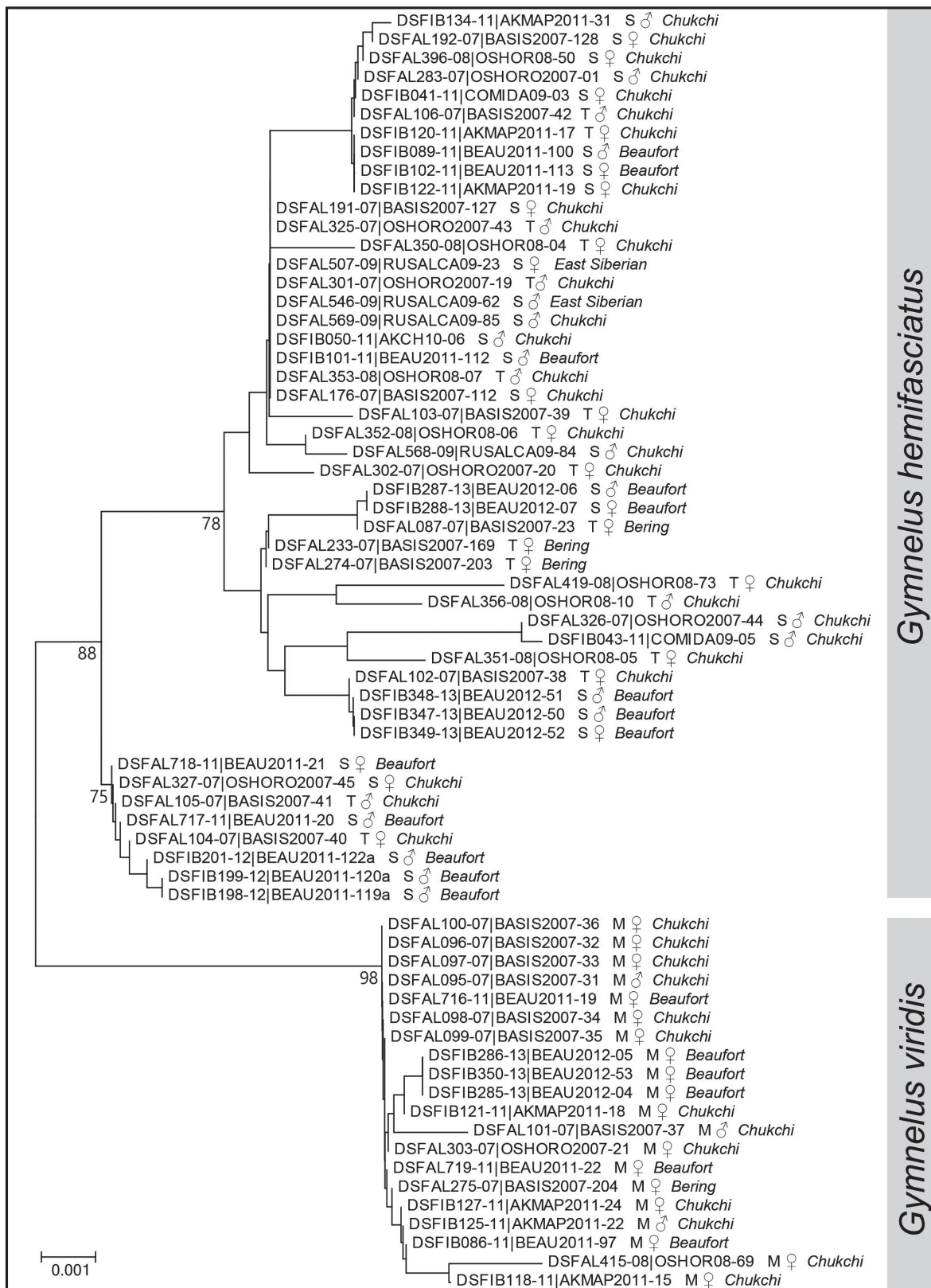
Coloration. The fresh sample (N = 221), including specimens barcoded as well as others examined, comprised 179 (81%) *G. hemifasciatus* and 42 *G. viridis* (19%). The coloration of the specimens indicated three morphotypes: two which are sexually dimorphic morphotypes of *G. hemifasciatus* and one sexually dimorphic morphotype of *G. viridis*.

The *G. hemifasciatus* sample included what we call the typical and the solid-band variations. Solid-banded *G. hemifasciatus* (Fig. 2) include full-banded males and half-banded females similar in coloration to that described for the nominal species *G. knipowitschi* by Chernova (1999a: male, fig. 1; female, fig. 3). The males have full dark bands extending ventrally to the anal fin, and the females have half bands not extending below midbody. The bands are solid, not broken by pale mottling or spots, and have relatively straight sides. The full-banded adult males all had black anal fins. The coloration in both sexes, except for the black anal fin, was evident even in very small specimens (Fig. 2) and the specimens could be sexed by coloration alone. The coloration of the females matched the description by Chernova for the females of *G. knipowitschi* (Chernova 1999a) as well as the holotype and paratype of *G. diporus* (Chernova 2000), which also were females. Of the 179 *G. hemifasciatus* specimens in the fresh sample, 85 (47.5%) were the solid-banded form. Of those, 37 (43.5%) were full-banded males and 48 (56.5%) were half-banded females.

The coloration of the form we refer to as the typical morphotype of *G. hemifasciatus* (Fig. 3) is similar to that described by Andriashev (1937: holotype, fig. 23) as *G. hemifasciatus* and by Chernova (1999a), in part, as *G. hemifasciatus* in her redescription of this species. It is called typical for its similarity to Andriashev's holotype, although it is not necessarily typical in the sense of being the most common morphotype. Both males and females of the typical morphotype are variegated, with full bands reaching the anal fin anteriorly, bands transitioning to a checkered or indistinct pattern posteriorly, and mottling on the head, nape, and, usually, all along the dorsum. The coloration is evident even in very small juveniles of both sexes and discrimination between males and females only becomes obvious externally when the males turn orange and develop black anal fins (Fig. 3). Chernova (1999a:7) included this pattern of coloration, although not the colors themselves, in the diagnosis of the redescribed *G. hemifasciatus* ("Coloration with dark transversal bands disappears toward the tail"). Of the 179 *G. hemifasciatus* in the fresh sample, 94 (52.5%) were the typical morphotype; 31 (33%) of those were males and 63 (67%) were females.

Males and females of *G. viridis* in the fresh sample (Fig. 4) had broad dark bands mottled with white, similar to Anderson's (1982) type 3. Coloration was most similar to that shown and described for *G. bilabrus* by Andriashev (1937: fig. 20) and Chernova (1998a: fig. 2a,b). In fresh condition, females were ivory colored with reddish brown bands mottled with white or ivory. The adult males were dark grayish brown with darker, almost black, broad mottled bands on the body, orange head, and orange and black pectoral fins (Fig. 4). The mottled bands were indistinct and not clearly discernible from the dark background color in adult males. In preservative the orange color turns pale gray.

None of the other color variations of *G. viridis* observed in Anderson's (1982) material or in the specimens from the Canadian high Arctic collected by Green & Mitchell (1997) were observed in our fresh sample. Anderson's (1982) specimens (Table 2) included many from more regions around the Arctic and more coloration variants than those of our fresh sample. Some differences could be due to the indistinct coloration in older preserved specimens but some also to true regional differences. For instance, in the fresh sample specimens from the Beaufort Sea were from the western (Alaskan) area of the sea only, and variation in coloration in *G. viridis* has been observed to be greater in the eastern (Canadian) part of the Beaufort Sea (e.g., Green & Mitchell 1997; Mecklenburg, unpubl.).



Gymnelus hemifasciatus

Gymnelus viridis

FIGURE 1. Neighbor-joining tree for 67 COI sequences of *Gymnelus hemifasciatus* and *G. viridis* collected in 2007–2012 from the Bering, East Siberian, Chukchi, and Beaufort seas. The Barcode of Life Datasystem (BOLD) process ID number, sample number as submitted to BOLD, coloration, sex, and ocean region are given. All *G. viridis* are the mottled-band morphotype (M). The *G. hemifasciatus* sample includes the typical morphotype (T) and the solid-band morphotype (S). The morphotypes are described in the text and shown in Figs. 2–4. Numbers below nodes represent bootstrap values (only values above 75 are shown). The scale bar represents K2P distance.

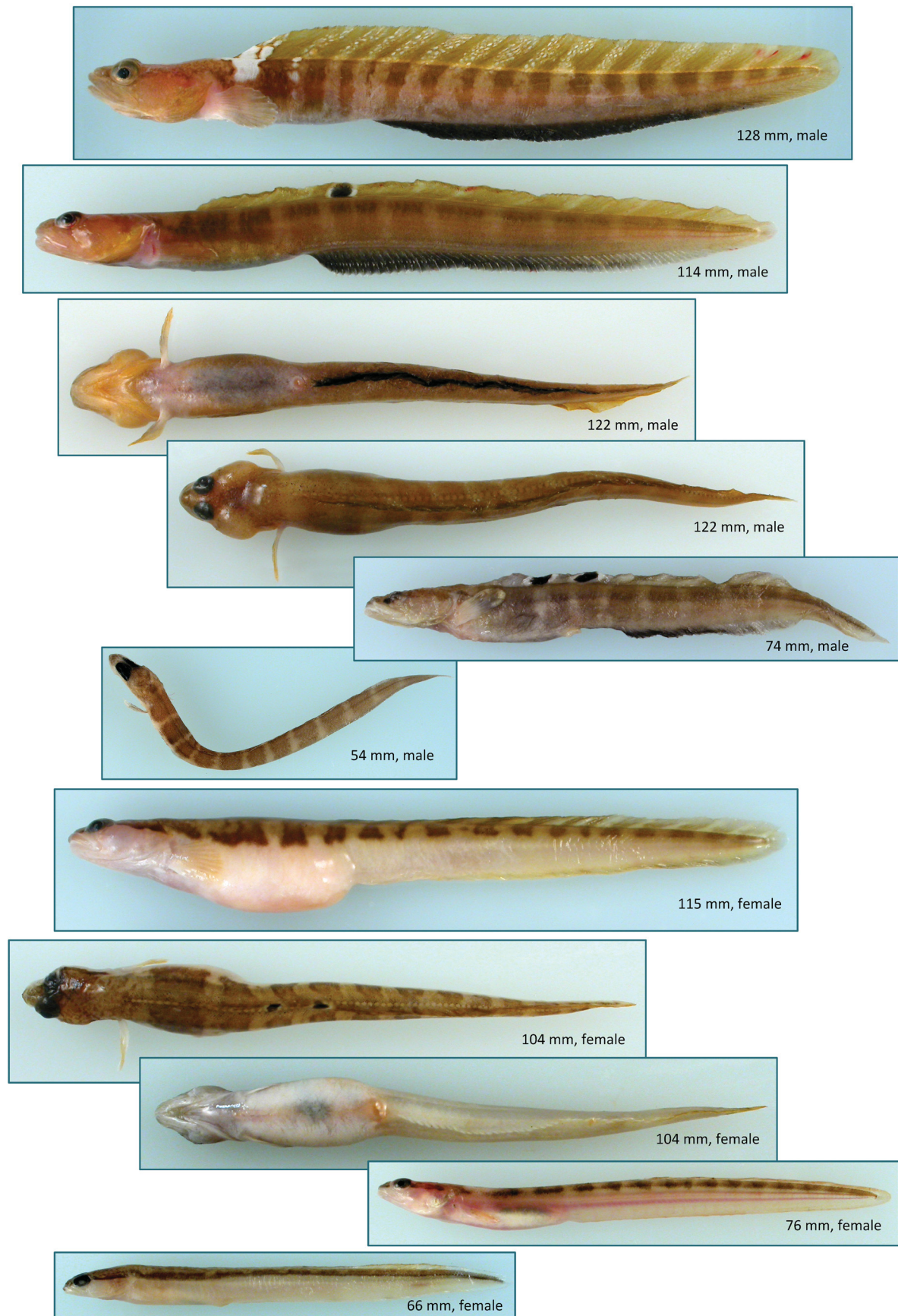


FIGURE 2. Examples of the solid-band morphotype of *Gymnelus hemifasciatus* in the fresh sample.

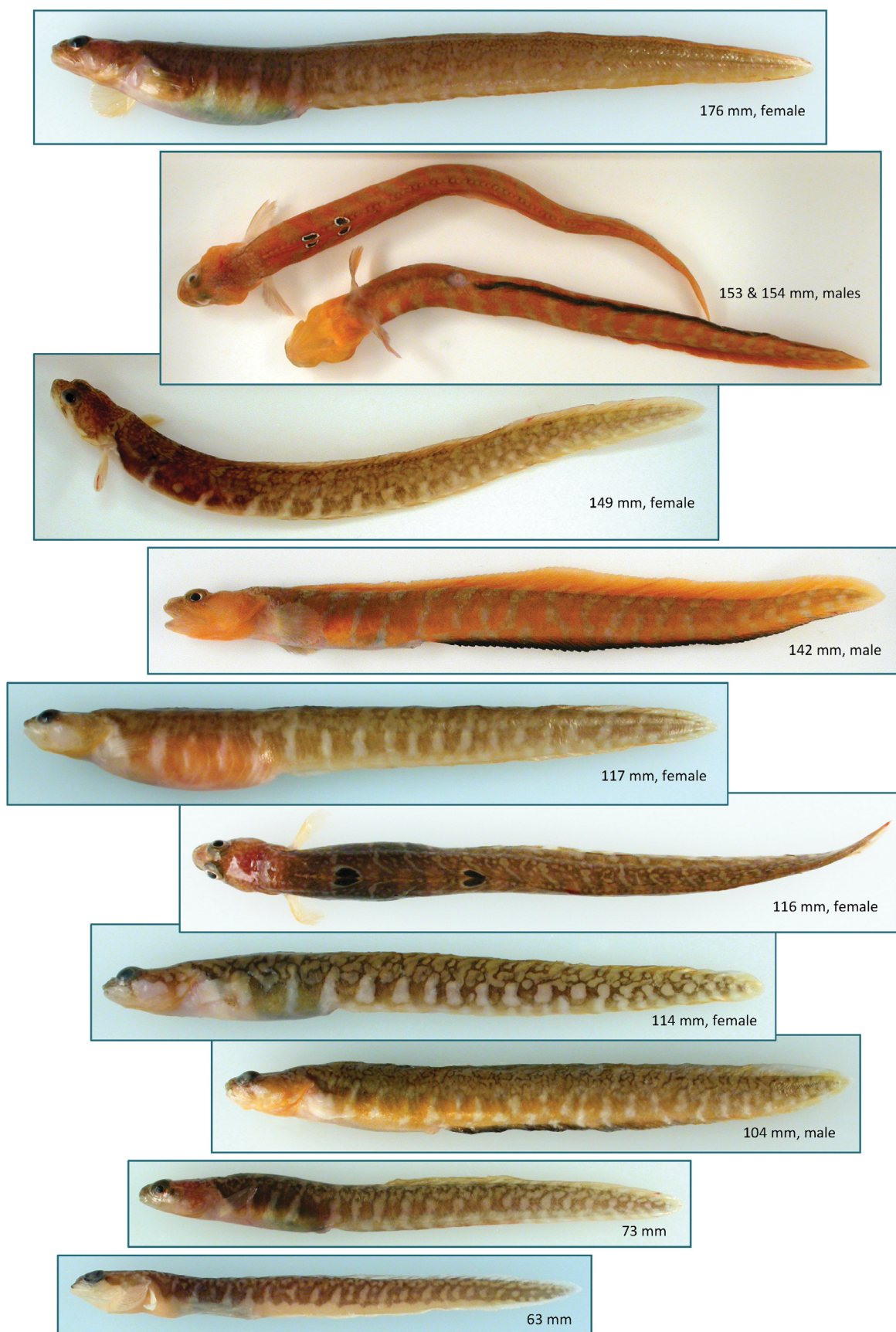


FIGURE 3. Examples of the typical morphotype of *Gymnelus hemifasciatus* in the fresh sample.

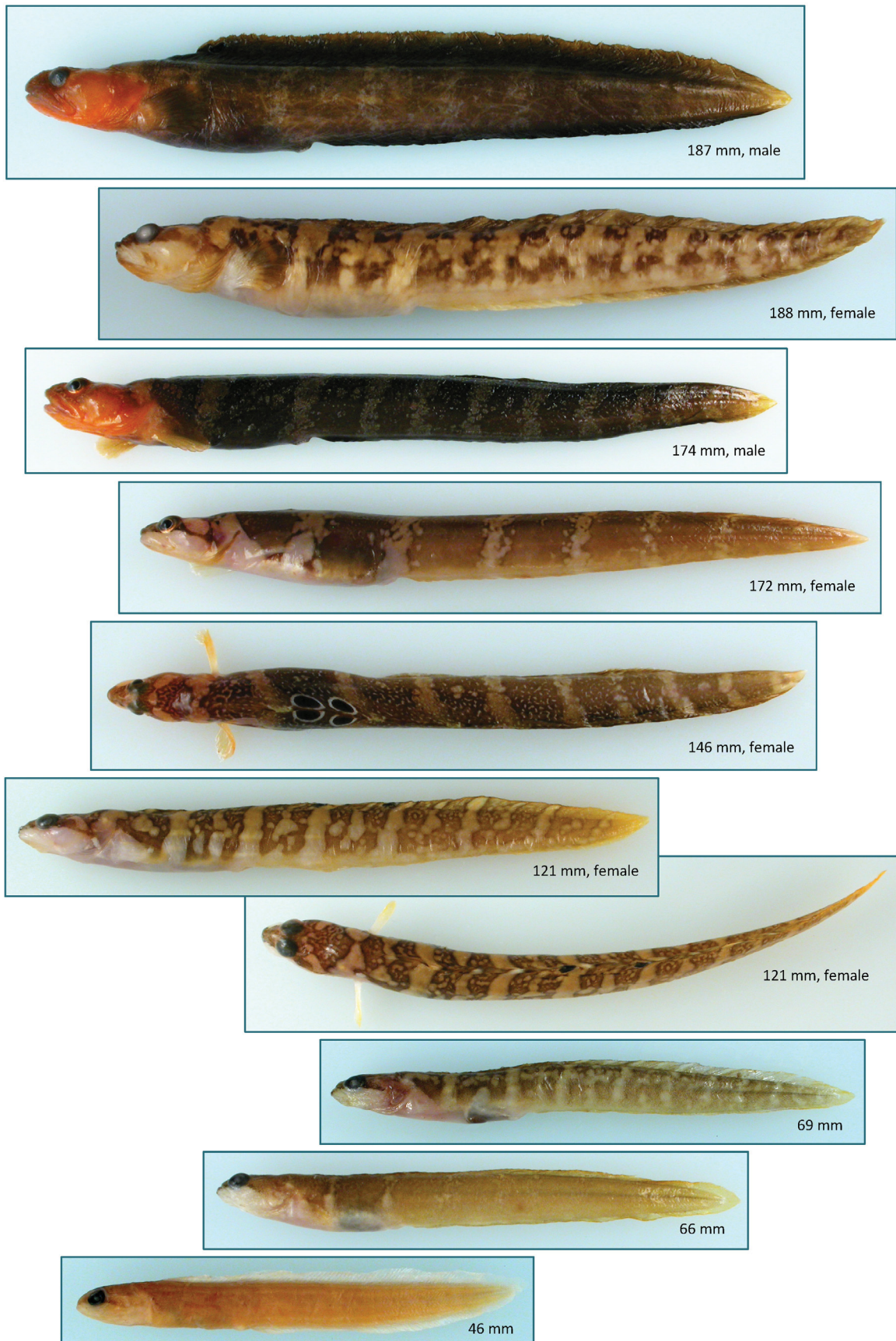


FIGURE 4. Examples of *Gymnelus viridis* in the fresh sample. All were the mottled-band morphotype.

TABLE 1. Successfully barcoded specimens of *Gymnelus hemifasciatus* and *G. viridis* collected from the East Siberian, Chukchi, Beaufort, and northern Bering seas from 2007 through 2012.

Species	Locality	Latitude	Longitude	Date collected	Catalog number	BOLD ID	Barcode ID	GenBank no.
<i>G. hemifasciatus</i>	East Siberian Sea	70.413	178.212	7-Sep-2009	CAS 228491-01	DSFAL507-09	RUSALCA09-23	GU804867
<i>G. hemifasciatus</i>	NE Bering Sea	65.647	-168.412	4-Sep-2007	CAS 230047	DSFAL083-07	BASIS2007-23	HQ712388
<i>G. hemifasciatus</i>	NE Chukchi Sea	69.999	-168.405	5-Sep-2007	CAS 230054-01	DSFAL102-07	BASIS2007-40	HQ712391
<i>G. hemifasciatus</i>	NE Chukchi Sea	69.999	-168.405	5-Sep-2007	CAS 230054-02	DSFAL103-07	BASIS2007-41	HQ712392
<i>G. hemifasciatus</i>	NE Chukchi Sea	69.999	-168.405	5-Sep-2007	CAS 230054-03	DSFAL104-07	BASIS2007-42	HQ712393
<i>G. hemifasciatus</i>	NE Chukchi Sea	69.999	-168.405	5-Sep-2007	CAS 230054-04	DSFAL105-07	BASIS2007-38	HQ712389
<i>G. hemifasciatus</i>	NE Chukchi Sea	69.999	-168.405	5-Sep-2007	CAS 230054-05	DSFAL106-07	BASIS2007-39	HQ712390
<i>G. hemifasciatus</i>	NE Chukchi Sea	69.504	-168.025	8-Sep-2007	CAS 230107-01	DSFAL176-07	BASIS2007-112	HQ712394
<i>G. hemifasciatus</i>	NE Chukchi Sea	69.223	-167.000	8-Sep-2007	CAS 230115-01	DSFAL191-07	BASIS2007-127	HQ712395
<i>G. hemifasciatus</i>	NE Chukchi Sea	69.223	-167.000	8-Sep-2007	CAS 230115-02	DSFAL192-07	BASIS2007-128	HQ712396
<i>G. hemifasciatus</i>	NE Bering Sea	66.008	-168.483	12-Sep-2007	CAS 230155	DSFAL233-07	BASIS2007-169	HQ712397
<i>G. hemifasciatus</i>	NE Bering Sea	64.492	-170.441	15-Sep-2007	CAS 230181-02	DSFAL274-07	BASIS2007-203	HQ712398
<i>G. hemifasciatus</i>	NE Chukchi Sea	70.193	-166.229	9-Aug-2007	CAS 230299	DSFAL283-07	OSHO2007-01	HQ712399
<i>G. hemifasciatus</i>	NE Chukchi Sea	70.898	-164.567	12-Aug-2007	CAS 230316-01	DSFAL302-07	OSHO2007-20	HQ712401
<i>G. hemifasciatus</i>	NE Chukchi Sea	70.898	-164.567	12-Aug-2007	CAS 230316-02	DSFAL301-07	OSHO2007-19	HQ712400
<i>G. hemifasciatus</i>	SE Chukchi Sea	68.182	-167.234	7-Aug-2007	CAS 230342-06	DSFAL325-07	OSHO2007-43	HQ712402
<i>G. hemifasciatus</i>	NE Chukchi Sea	70.811	-163.279	12-Aug-2007	CAS 230343-03	DSFAL327-07	OSHO2007-45	HQ712404
<i>G. hemifasciatus</i>	NE Chukchi Sea	70.811	-163.279	12-Aug-2007	CAS 230343-07	DSFAL326-07	OSHO2007-44	HQ712403
<i>G. hemifasciatus</i>	W Beaufort Sea	71.028	-150.100	22-Sep-2012	CAS 236448-03	DSFIB287-13	BEAU2012-06	KM987632
<i>G. hemifasciatus</i>	W Beaufort Sea	71.028	-150.100	22-Sep-2012	CAS 236449-03	DSFIB288-13	BEAU2012-07	KM987637
<i>G. hemifasciatus</i>	NE Chukchi Sea	71.489	-163.373	22-Aug-2009	UAM 2908-02	DSFIB041-11	COMIDA09-03	KM987615
<i>G. hemifasciatus</i>	W Beaufort Sea	71.171	-151.100	28-Sep-2012	UAM 3696	DSFIB347-13	BEAU2012-50	KM987621

....continued on the next page

TABLE 1. (Continued)

Species	Locality	Latitude	Longitude	Date collected	Catalog number	BOLD ID	Barcode ID	GenBank no.
<i>G. hemifasciatus</i>	W Beaufort Sea	71.326	-151.100	28-Sep-2012	UAM 3697	DSFIB248-13	BEAU2012-51	KM987626
<i>G. hemifasciatus</i>	W Beaufort Sea	71.028	-150.100	22-Sep-2012	UAM 3698	DSFIB349-13	BEAU2012-52	KM987631
<i>G. hemifasciatus</i>	NW Chukchi Sea	71.440	-174.861	17-Sep-2009	UAM 5520	DSFAL568-09	RUSALCA09-84	GU804880
<i>G. hemifasciatus</i>	NW Chukchi Sea	71.418	-174.814	17-Sep-2009	UAM 5521	DSFAL569-09	RUSALCA09-85	GU804881
<i>G. hemifasciatus</i>	NE Chukchi Sea	70.060	-167.164	8-Jul-2008	UAM 5752	DSFAL396-08	OSHOR08-50	HQ712410
<i>G. hemifasciatus</i>	SE Chukchi Sea	66.202	-168.659	7-Jul-2008	UAM 5804-01	DSFAL356-08	OSHOR08-10	HQ712409
<i>G. hemifasciatus</i>	SE Chukchi Sea	68.187	-167.197	12-Jul-2008	UAM 5831-01	DSFAL350-08	OSHOR08-04	HQ712405
<i>G. hemifasciatus</i>	SE Chukchi Sea	68.187	-167.197	12-Jul-2008	UAM 5831-02	DSFAL351-08	OSHOR08-05	HQ712406
<i>G. hemifasciatus</i>	SE Chukchi Sea	68.187	-167.197	12-Jul-2008	UAM 5831-07	DSFAL352-08	OSHOR08-06	HQ712407
<i>G. hemifasciatus</i>	SE Chukchi Sea	68.187	-167.197	12-Jul-2008	UAM 5831-08	DSFAL353-08	OSHOR08-07	HQ712408
<i>G. hemifasciatus</i>	SE Chukchi Sea	66.202	-168.659	7-Jul-2008	UAM 5994	DSFAL419-08	OSHOR08-73	HQ712411
<i>G. hemifasciatus</i>	W Beaufort Sea	70.452	-145.088	17-Aug-2011	UAM 6271-01	DSFAL718-11	BEAU2011-21	KM987616
<i>G. hemifasciatus</i>	W Beaufort Sea	70.452	-145.088	17-Aug-2011	UAM 6271-02	DSFAL717-11	BEAU2011-20	KM987635
<i>G. hemifasciatus</i>	NE Chukchi Sea	71.489	-163.373	23-Aug-2009	UAM 6295	DSFIB043-11	COMIDA09-05	KM987618
<i>G. hemifasciatus</i>	W Beaufort Sea	70.960	-149.572	23-Aug-2011	UAM 6296-01	DSFIB199-12	BEAU2011-120	KM987619
<i>G. hemifasciatus</i>	W Beaufort Sea	70.960	-149.572	23-Aug-2011	UAM 6296-02	DSFIB198-12	BEAU2011-119	KM987633
<i>G. hemifasciatus</i>	W Beaufort Sea	70.960	-149.572	23-Aug-2011	UAM 6297	DSFIB201-12	BEAU2011-122	KM987642
<i>G. hemifasciatus</i>	NE Chukchi Sea	69.820	-163.881	24-Aug-2010	UAM 6331	DSFIB050-11	AKCH10-06	KM987641
<i>G. hemifasciatus</i>	W Beaufort Sea	71.734	-153.526	28-Aug-2011	UAM 6345-01	DSFIB102-11	BEAU2011-113	KM987625
<i>G. hemifasciatus</i>	W Beaufort Sea	71.734	-153.526	28-Aug-2011	UAM 6345-02	DSFIB101-11	BEAU2011-112	KM987623
<i>G. hemifasciatus</i>	W Beaufort Sea	71.593	-155.037	31-Aug-2011	UAM 6389-02	DSFIB089-11	BEAU2011-100	KM987639
<i>G. hemifasciatus</i>	NE Chukchi Sea	71.300	-157.204	5-Sep-2011	UAM 6458	DSFIB120-11	AKMAP2011-17	KM987627
<i>G. hemifasciatus</i>	NE Chukchi Sea	71.160	-160.193	7-Sep-2011	UAM 6480	DSFIB134-11	AKMAP2011-31	KM987620

..... continued on the next page

TABLE 1. (Continued)

Species	Locality	Latitude	Longitude	Date collected	Catalog number	BOLD ID	Barcode ID	GenBank no.
<i>G. hemifasciatus</i>	NE Chukchi Sea	71.166	-160.211	7-Sep-2011	UAM 6482-01	DSFIB122-11	AKMAP2011-19	KM987634
<i>G. hemifasciatus</i>	East Siberian Sea	71.650	179.550	11-Sep-2009	ZIN uncataloged	DSFAL546-09	RUSALCA09-62	GU804875
<i>G. viridis</i>	NE Chukchi Sea	69.999	-168.405	5-Sep-2007	CAS 230053-01	DSFAL097-07	BASIS2007-35	HQ712416
<i>G. viridis</i>	NE Chukchi Sea	69.999	-168.405	5-Sep-2007	CAS 230053-02	DSFAL098-07	BASIS2007-34	HQ712415
<i>G. viridis</i>	NE Chukchi Sea	69.999	-168.405	5-Sep-2007	CAS 230053-03	DSFAL099-07	BASIS2007-33	HQ712414
<i>G. viridis</i>	NE Chukchi Sea	69.999	-168.405	5-Sep-2007	CAS 230055-01	DSFAL095-07	BASIS2007-36	HQ712417
<i>G. viridis</i>	NE Chukchi Sea	69.999	-168.405	5-Sep-2007	CAS 230055-02	DSFAL096-07	BASIS2007-37	HQ712418
<i>G. viridis</i>	NE Chukchi Sea	69.999	-168.405	5-Sep-2007	CAS 230055-03	DSFAL100-07	BASIS2007-32	HQ712413
<i>G. viridis</i>	NE Chukchi Sea	69.999	-168.405	5-Sep-2007	CAS 230055-04	DSFAL101-07	BASIS2007-31	HQ712412
<i>G. viridis</i>	NE Bering Sea	64.492	-170.441	15-Sep-2007	CAS 230182-05	DSFAL275-07	BASIS2007-204	HQ712419
<i>G. viridis</i>	NE Chukchi Sea	70.898	-164.567	12-Aug-2007	CAS 230317	DSFAL303-07	OSHORO2007-21	HQ712420
<i>G. viridis</i>	NE Chukchi Sea	70.839	-160.686	9-Sep-2011	CAS 235295	DSFIB125-11	AKMAP2011-22	KM987614
<i>G. viridis</i>	W Beaufort Sea	71.028	-150.100	22-Sep-2012	CAS 236447-01	DSFIB286-13	BEAU2012-05	KM987640
<i>G. viridis</i>	W Beaufort Sea	71.217	-150.100	22-Sep-2012	UAM 2980	DSFIB285-13	BEAU2012-04	KM987638
<i>G. viridis</i>	W Beaufort Sea	71.028	-150.100	22-Sep-2012	UAM 3699	DSFIB350-13	BEAU2012-53	KM987624
<i>G. viridis</i>	SE Chukchi Sea	66.202	-168.659	7-Jul-2008	UAM 5989	DSFAL415-08	OSHOR08-69	HQ712422
<i>G. viridis</i>	W Beaufort Sea	70.452	-145.088	17-Aug-2011	UAM 6272	DSFAL719-11	BEAU2011-22	KM987630
<i>G. viridis</i>	W Beaufort Sea	70.670	-145.104	17-Aug-2011	UAM 6275	DSFAL716-11	BEAU2011-19	KM87636
<i>G. viridis</i>	W Beaufort Sea	71.246	-153.117	1-Sep-2011	UAM 6417-02	DSFIB086-11	BEAU2011-97	KM987629
<i>G. viridis</i>	NE Chukchi Sea	71.300	-157.204	5-Sep-2011	UAM 6459-01	DSFIB121-11	AKMAP2011-18	KM987617
<i>G. viridis</i>	NE Chukchi Sea	71.300	-157.204	5-Sep-2011	UAM 6459-02	DSFIB127-11	AKMAP2011-24	KM987628
<i>G. viridis</i>	NE Chukchi Sea	71.224	-157.983	6-Sep-2011	UAM 6473-01	DSFIB118-11	AKMAP2011-15	KM987622

TABLE 2. Distribution of occipital (supratemporal) pores and three color patterns in *Gymnelus viridis* around the Arctic from data in Anderson (1982). N is the number of specimens.

Region	Number of occipital pores						Color patterns			
	0	1	2	3	4	N	Monotone	Mottled bands	Solid bands	N
Greenland	1	0	75	6	2	84	6	23	6	35
Eastern Canada	3	0	21	46	3	73	18	25	10	53
Beaufort and Chukchi seas	3	0	15	39	0	57	13	29	10	52
Bering Sea	0	0	0	22	1	23	7	13	9	29
Siberian seas	2	0	2	6	0	10	4	5	1	10
Total specimens	9	0	113	119	6	247	48	95	36	179
Standard length (mm)							56–242	39–192	32–179	

As in previous studies (e.g., Anderson 1982), in both *G. hemifasciatus* and *G. viridis* in the fresh sample one or more black spots bordered with white (ocelli) were sometimes present on the dorsal fin. No difference in the frequency or position of ocelli was found among the morphotypes or sexes.

Occipital pores and supratemporal commissure. The postorbital (temporal) pores showed little variation in the fresh sample and Anderson's (1982) sample, with nearly all exhibiting four pores bilaterally, and further reporting is restricted to the occipital (supratemporal) pores. They were observed in 204 specimens of the fresh sample (Table 3). No appreciable differences between males and females were found so they are grouped in Table 3. The majority (60.0%) of specimens of the solid-band *G. hemifasciatus* morphotype had two occipital pores (pattern 1-0-1) and an incomplete commissure, followed by 22.7% with three pores (pattern 1-1-1) and a complete commissure. Other patterns appeared to be related to failure of pores to open externally in young specimens. Most (88.8%) of the typical morphotype of *G. hemifasciatus* had three occipital pores and 4.5% had two with the median pore missing. The rest had various combinations with a pore doubled or others missing.

TABLE 3. Occipital (supratemporal) pore counts and lengths of 204 specimens of *Gymnelus hemifasciatus* and *G. viridis* in the fresh sample.

Variable	<i>G. hemifasciatus</i> , typical morphotype		<i>G. hemifasciatus</i> , solid-band morphotype		<i>G. viridis</i>	
	N	%	N	%	N	%
Occipital pore counts						
1-1-1	79	88.8	17	22.7	38	95.0
1-0-1	4	4.5	45	60.0	0	0.0
1-0-0 or 0-0-1	2	2.3	7	9.3	0	0.0
0-0-0	1	1.1	6	8.0	0	0.0
0-1-1 or 1-1-0	1	1.1	0	0.0	0	0.0
2-1-1	2	2.3	0	0.0	1	2.5
1-2-1	0	0.0	0	0.0	1	2.5
Total specimens	89	100.1	75	100.0	40	100.0
Total length (mm)	63–176		50–159		45–256	
Standard length (mm)	60–163		48–144		42–220	

In data from Anderson (1982), no clear pattern regionally was seen for *G. viridis* in the number of occipital pores except for a tendency for two pores around Greenland, three pores in the Bering Sea, and either two or three pores in eastern Canadian waters and the Beaufort and Chukchi seas (Table 2). In the fresh sample, primarily from

the Beaufort and Chukchi seas, nearly all (95.0%) *G. viridis* had three pores with complete supratemporal commissures (Table 3). This shows that in order to understand coloration, sex, the supratemporal commissure and its pores, and geography one needs a very large sample size.

Distribution of the fresh sample. The geographic distributions of *G. viridis* and the two morphotypes of *G. hemifasciatus* in the fresh sample are shown in Fig. 5. In all, *Gymnelus* specimens taken at 60 stations from 2004 to 2013 are represented. *Gymnelus viridis* was taken at 20 (33%) of those stations, the typical morphotype of *G. hemifasciatus* at 18 (30%), and the solid-band morphotype at 36 (60%). Although it appears from the maps that the solid-band morphotype of *G. hemifasciatus* mostly occurs more northerly than the typical morphotype, this could be an artifact of the sample. The solid-band morphotype also occurs in more southerly locations (e.g., Balushkin *et al.* 2011). It could also reflect preference for different environmental conditions. For instance, sediments with a high proportion of sand are more typical of the southern part of the sampling area (Fig. 5).

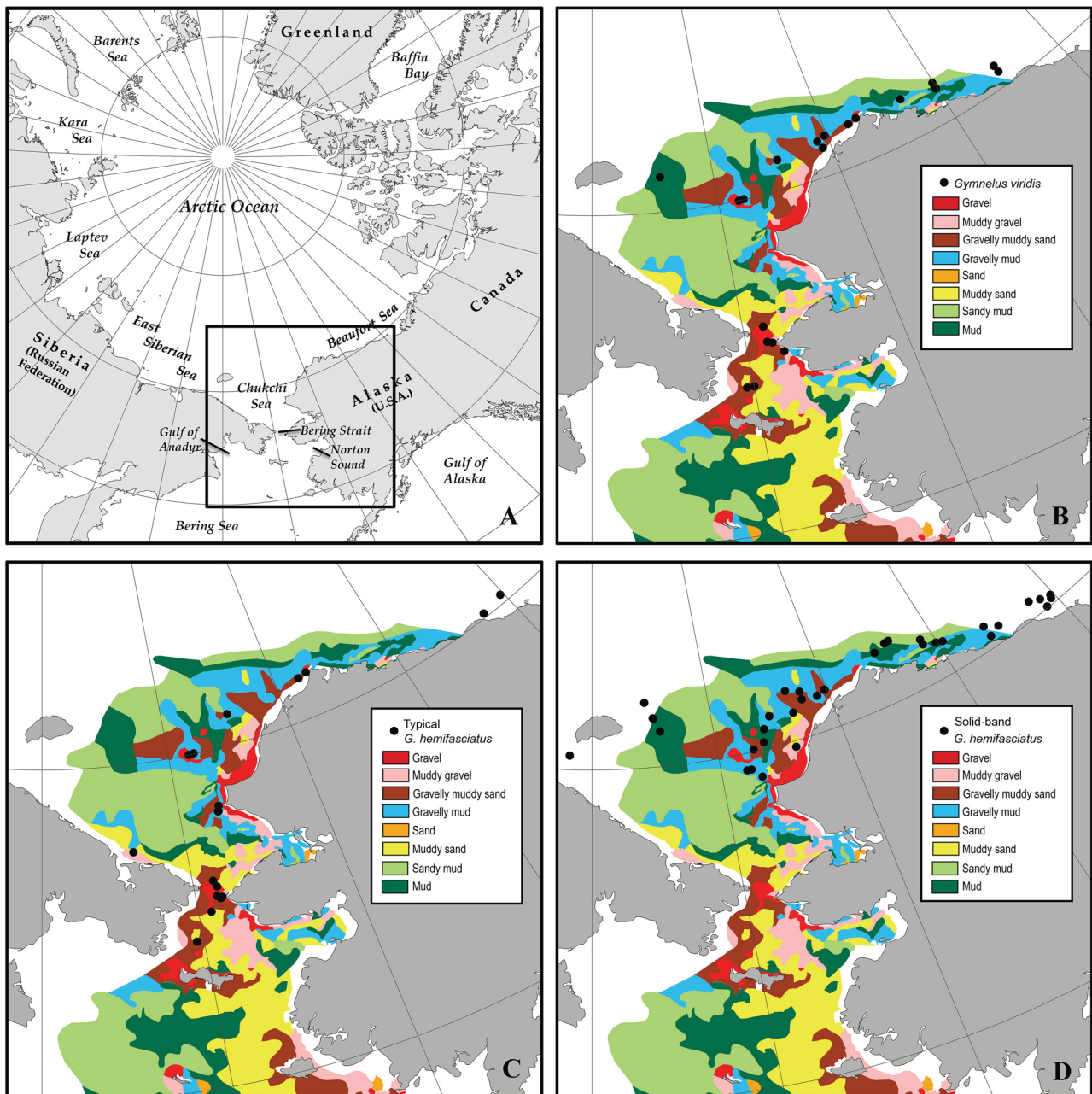


FIGURE 5. Distribution of *Gymnelus* specimens in the fresh sample on bottom sediments. A, index map. B, *G. viridis*. C, typical morphotype of *G. hemifasciatus*. D, solid-band morphotype of *G. hemifasciatus*. Sediment map based on data from U.S. Department of Commerce, NOAA (1987).

More specimens of the typical morphotype of *G. hemifasciatus* are included in the fresh sample but the solid-band morphotype was taken at twice as many stations (Table 4). The typical morphotype was often represented by greater numbers per haul than the solid-banded one, but being museum voucher specimens, the sample is probably biased.

TABLE 4. Summary of bottom depth, temperature, and salinity at stations where *Gymnelus* specimens in the fresh sample were taken by bottom trawls and for which the environmental data are available.

Environmental variable	<i>G. hemifasciatus</i> , typical morphotype		<i>G. hemifasciatus</i> , solid-band morphotype		<i>G. viridis</i>	
	Range	No. stations	Range	No. stations	Range	No. stations
Depth (m)	32–100	18	33–101	36	20–100	20
Temperature (°C)	–1.5 to 10.5	14	–1.8 to 6.9	29	–1.8 to 10.5	18
Salinity	30.62–32.90	14	31.25–33.44	29	28.73–33.44	18

Gymnelus viridis was frequently taken in the same hauls with one or the other morphotype of *G. hemifasciatus*. In contrast, the two morphotypes of *G. hemifasciatus* were taken together in the same tow only once. In that instance (UAM 47835) a female of the typical morphotype ready to spawn was taken with two females (half-banded) and a juvenile male (full-banded) of the solid-band form. The spawning female had 1-1-1 occipital pores, one half-banded female had 1-0-1, the other half-banded female had 1-1-1, and the juvenile male had 1-0-1. That one odd catch was at a depth of 100 m and was the only one where the typical form of *G. hemifasciatus* was taken so deep.

Taken at face value the maximum depths for the two morphotypes of *G. hemifasciatus* are similar (Table 4). However, only one typical *G. hemifasciatus* was taken at 100 m (1 of 18 stations, 6%); the others were taken at depths of 60 m or less (17 of 18 stations, 94%). The solid-band form was caught more often (8 of 36 stations, 22%) at depths greater than 60 m, to 101 m. It also was caught more often at negative temperatures (14 of 29 stations with temperature data, 48%) than the typical form (2 of 14 stations, 14%). *Gymnelus viridis* is reported to be a shallower-water species than *G. hemifasciatus* (e.g., Anderson 1982; Mecklenburg *et al.* 2002) and this was reflected in *G. viridis* being caught at the shallowest, least saline stations and less frequently at negative temperatures. Temperatures were negative at only 3 of the 19 stations (15%) where *G. viridis* was taken.

The information on substrate from observation of net contents, grain size in sediment grabs, and observations by remotely operated vehicle at the stations where *Gymnelus* were taken is incomplete and difficult to assess. Most sites had high proportions of sand and mud in various combinations, which is characteristic of the region. Net contents indicated that the solid-band morphotype of *G. hemifasciatus* tended to be found on substrates with a high proportion of mud mixed with some combination of sandy mud, gravel, and shell hash, whereas the typical morphotype was more often associated with muddy sand and rougher substrate including shell hash, gravel, rock, cobble, and boulders. *Gymnelus viridis* was most often taken on the rougher substrates, and more often with the typical form of *G. hemifasciatus* (nine stations) than with the solid-band form (four stations). The same impression was gained from plots of the collection localities on a map of sediment types (Fig. 5). A few localities fell outside the areas for which the sediments have been mapped, but of the 18 localities for *G. viridis* that were on mapped sediments, 15 (83%) were on gravelly substrate (Fig. 5B). All 16 (100%) of the locations with sediment data for the typical morphotype of *G. hemifasciatus* were on gravelly substrate, and none on mud or sand without gravel (Fig. 5C). All 27 (100%) of the localities for the solid-band morphotype of *G. hemifasciatus* that are within mapped sediment areas had a high proportion of mud; 13 (48%) were on smooth mud, sandy mud, or muddy sand without gravel and none on primarily gravel substrate (gravel or muddy gravel; Fig. 5D).

Review of the nominal forms. Below we assess each of Chernova’s new names on the basis of her diagnostic and other identifying characters. A major difficulty in assessing these nominal forms has been the inconsistency in her unquantified diagnostic characters from one form to another. The diagnoses reflect an arbitrariness in choosing characters which we demonstrate in Tables 5 and 6. In boldface type are those characters used in Chernova’s diagnoses (mostly given as the quantified character value from the descriptive part, rather than, e.g., “eye large” or “small gill opening”) and those in regular typeface are those used in diagnoses of other nominal forms not used in all, taken also from the descriptive parts of those forms. As will be shown, many of the characters often were based on ontogenetic or sexually polymorphic features.

TABLE 5. Diagnostic and other identifying characters of nominal forms of *Gymnelus hemifasciatus*. Boldface type indicates values given as diagnostic; other values are from the descriptions of type specimens (Chernova 1999a, 2000).

Character	<i>G. knipowitschi</i> N = 14: 67–142 mm TL	<i>G. diporus</i> N = 2: 79, 107 mm TL	<i>G. soldatovi</i> N = 5: 101–111 mm TL
Supratemporal commissure	Incomplete	Incomplete	Complete
Color bands, number	14–15	“Up to 18”	0 (dorsal mottling)
Predorsal length, % TL	17–21	18.2–18.9	16.4–19.2
Head width, % HL	48–58	50.0–55.6	46.0–58.0
Eye diameter, % HL	22.6–29.8	23.8–24.4	22.3–25.0
Snout length, % HL	21.8–26.1	16.9–20.8	23.7–25.8
Gill slit length, % HL	18.2–26.7	23.1–25.0	23.5–28.1
Pectoral fin length, % HL	41.0–53.0	53.6–54.0	44.0–53.0
Pectoral base height, % P length	37.0–50.0	40.0–42.0	35.0–45.0
Retrorse dorsal fin origin?	No	No	No
Free dorsal fin pterygiophores	0–2	Not given	0–1
Vertebrae, total	86–94	88–94	88–94

Gymnelus hemifasciatus Andriashev 1937

(Figs. 2 and 3)

Three nominal species were erected that we consider variant phenotypes of *G. hemifasciatus*: *G. knipowitschi* Chernova 1999a, *G. diporus* Chernova 2000, and *G. soldatovi* Chernova 2000 (Table 5).

Gymnelus knipowitschi, described from 14 types with 73 other specimens listed, basically distributed from the Barents Sea eastward to Arctic Canada including the Bering Sea, was diagnosed by having an incomplete supratemporal commissure, 14–15 dark transverse bars, 0–2 free dorsal-fin pterygiophores, 86–94 vertebrae, and several morphometric characters overlapping with other nominal forms (Table 5). Head width and length are often sexually dimorphic in many eelpouts (e.g., some Atlantic *Lycenchelys* [Goode & Bean 1896, figs. 277, 278, 282]; *Gymnelus* [Anderson 1982]; *Pachycara brachycephalum* [Anderson 1988]). Both head length and width are sexually dimorphic in *G. hemifasciatus* (Anderson 1982) but this is not discussed by Chernova (1999a, 2000), probably owing to her small sample sizes. We found a mistranslation in the English language version of Chernova (1999a:2) that reads “Head wide and shallow (wider than longer)” that should read (our translation) “. . . (wider than deep)”. A “large” eye was purported to be sexually dimorphic, but with greatly overlapping values between the sexes; the values are statistically insignificant at N = 14 (Chernova 1999a:2). Pectoral fin length was also purported to be sexually dimorphic based on the same sample.

Gymnelus diporus, described from two females, a juvenile and a subadult from the Commander Islands and the Pacific Ocean off southeastern Kamchatka, was diagnosed in having an incomplete supratemporal commissure as above, in not having a posteriorly shifted dorsal fin origin (the same in both *G. knipowitschi* and *G. soldatovi*), a narrow and long pectoral fin, short snout, up to 18 vertical bands, and small size (up to 107 mm TL, but N = 2). Compared to *G. knipowitschi* we find only a shorter snout length non-overlapping in these two specimens (Table 5) among Chernova’s (1999a, 2000) characters. However, we discern no significant differences in the one illustration (Chernova 2000: fig. 4) of this form with either *G. knipowitschi* or *G. soldatovi* (Chernova 1999a: figs. 1, 3; Chernova 2000: fig. 1) and ascribe the difference in snout lengths to perhaps accuracy of measurement due to preservation, or individual or ontogenetic variation. Compared to *G. soldatovi* only the complete supratemporal commissure, lack of well-defined dark bands, and the snout length distinguish that form (Table 5). We refer to the *G. diporus* form as “half-banded” *G. hemifasciatus*, which are females of the solid-band morphotype (females half-banded, males full-banded).

Gymnelus soldatovi, described from five types and six other specimens from the Okhotsk Sea and Kuril Islands, was diagnosed in having a complete supratemporal commissure with three occipital pores, few vertebrae

(mistranslated in English version as a “high” vertebral number), cylindrical body, “wide” head, large snout, small gill opening, “wide” (meaning high base) pectoral fin, and small size (to 111 mm TL). Vertebral number, head width, snout length (except in *G. diporus*), gill slit length, and pectoral base height all overlap with the other two nominal forms (Table 5). We regard the feature “cylindrical body” a non-character reflecting either a preservation artifact in these pliable fishes, or general, individual robustness. A mistranslation in the English language edition of the description of *G. soldatovi* gives females with the black anal fin whereas Chernova (2000:10) in the original edition correctly states it is the males with this feature (our translation).

***Gymnelus viridis* (Fabricius 1780)**

(Fig. 4)

Four nominal species were erected that we consider variant phenotypes of *G. viridis*: *G. barsukovi* Chernova 1999b, *G. platycephalus* Chernova 1999b, *G. gracilis* Chernova 2000, and *G. obscurus* Chernova 2000.

Gymnelus barsukovi, described from 10 types and 13 other specimens from the Laptev Sea eastward to the Beaufort Sea including the northern Bering Sea, was diagnosed in having a complete supratemporal commissure with three occipital pores, “numerous” vertebrae, a cylindrical body, a “wide” head, “small” eye, “large” mouth (probably upper jaw length), large size, and uniform dark coloration. Vertebral number greatly overlaps that of the other nominal forms (Table 6). We consider “cylindrical body” a non-character as it can be biased by compaction during preservation of these pliable fishes, or it may be a reflection of an individual’s general robustness due to the larger size of this form. This also applies to head width, eye diameter, and upper jaw length (Table 6). We do not know the criteria of how Chernova (1999b:349) decided that individuals 156–187 mm were immature nor to which sex she was referring, but if females were examined they may simply have recently spawned. *Gymnelus viridis* females mature at about 110–120 mm SL, seen in a few mottled-band females by Anderson (1982:31) and shown here in Fig. 6.



FIGURE 6. Female *G. viridis* of the mottled-band, or “*G. bilabrus*,” morphotype, 12–13 cm in length, guarding her 5-day-old eggs. The fish was collected at Resolute, Cornwallis Island, central Arctic Canada, and bred and spawned at the Vancouver Aquarium, British Columbia, Canada. Photograph by Danny Kent, Vancouver Aquarium.

Gymnelus platycephalus, described from seven types and four other specimens from the Bering and Chukchi seas, was diagnosed in having a complete supratemporal commissure with three occipital pores, a “low, flat” head, “high, laterally compressed” body, “small” mouth, “low” number of jaw teeth, a “large” gill opening, small size, and adult males “with a closed mouth, the lower jaw fits inside the upper jaw” (or mouth subterminal). We consider the overlapping head depth and mouth size (upper jaw length) nondiagnostic as is body depth except in the juveniles described (see below) as *G. gracilis*. A “low number” of jaw teeth reflects an ontogenetically variable character in many zoarcids including *Gymnelus* (e.g., Anderson 1982, 1989, 1995), impossible to compare to other nominal forms as sizes were not given. We deem the subterminal mouth of males as nondiagnostic since Chernova’s female holotype shows a subterminal mouth as well (Chernova 1999b: fig. 8a). Coloration was described as including a “fine uniform netted-cellular pattern.” None of the material in our fresh sample fits the description of this form, although Chernova (2009a,b; pers. comm.) identified several of the RUSALCA specimens and several from other recent collections as *G. platycephalus* that we identify as *G. hemifasciatus*. None of our *G. hemifasciatus* or *G. viridis* in the fresh sample had coloration even remotely like the only illustration of *G. platycephalus* with a pattern (Chernova 1999b: fig. 8b), a preservative-faded adult male collected 11 September 1950 (Anderson 1982:73). Anderson recorded for the 1982 review, but did not elaborate, three specimens as “spotted” or “speckled” that closely fit this morphotype. One from Somerset Island, Arctic Canada (NMC 76-0102), had a complete supratemporal commissure with three occipital pores, and two specimens, one from southwestern Greenland (ZMUC uncatalogued, “specimen 26”) and one from Baffin Island, Canada (NMC 77-1501D), had incomplete commissures with two occipital pores.

Gymnelus gracilis, described from six juvenile specimens, 47–82 mm TL, from the Pacific Ocean off the coast of Kamchatka near Cape Afrika, was diagnosed in having an interrupted supratemporal commissure with two occipital pores, a “not” posteriorly shifted dorsal-fin origin, a very thin body, small head, few teeth, and coloration of “numerous (about 46) transverse dark bands.” The character “not having a posteriorly shifted dorsal-fin origin” is incorrect (unless being compared to *G. retrodorsalis*), as the dorsal origin is placed above the middle of the pectoral fin (Chernova 2000: fig. 5) and there are two free dorsal pterygiophores, a variable character, with the fin origin associated with vertebrae 4–6 (see Anderson 1994:13). We regard the head length and width, and slender body as ontogenetic features, with the lower values typical of juvenile eelpouts.

Gymnelus obscurus, described from three northwestern Bering Sea young adults, was diagnosed in having a complete supratemporal commissure with three occipital pores, a “large” gill opening, “small” eye, wide interorbital distance, “intense” pigmentation (body uniformly dark), and adult males with a subterminal mouth. Gill opening length (in these short openings) overlaps only with *G. barsukovi* but as the sample size for all these nominal forms is so small, we regard this as insignificant (Table 6). Eye diameter greatly overlaps the other nominal forms. Chernova (2000: fig. 7) has accurately depicted sexual dimorphism in head width, to which interorbital width is redundant (Table 6). None of the specimens in our fresh sample matches the diagnosis or description.

Gymnelus bilabrus was originally described from three specimens (Andriashev 1937) and redescribed by Chernova (1998a) from the holotype and eight nontypes collected from the Bering and Beaufort seas. Andriashev (1937) mainly distinguished *G. bilabrus* from *G. viridis* by its adnate upper lip (hence the name), which Anderson (1982:32) found in four additional *G. viridis* specimens, its deeper and narrower head, which Anderson (1982) showed were sexually dimorphic in *Gymnelus*, and its “marbled” (mottled) coloration. However, Andriashev (1937) reported one specimen was not of the marbled pattern but had “wide brown bars” and “irregular small and large light, dark-edged spots” (translation).

Among important characters used by Chernova (1998a), *G. bilabrus* was a form with a complete supratemporal commissure (as were all her *G. viridis* morphotypes except the juveniles named *G. gracilis*), the anterior placement of the dorsal fin origin (but predorsal length greatly overlapping the other forms), and the sexually dimorphic head length not overlapping in the juvenile *G. gracilis* form (Table 6). Chernova (1998a) compared *G. bilabrus* (9 specimens) with *G. viridis* (17 specimens), an inadequate sample size we believe, especially when total ranges of values of both meristic (such as pectoral-fin rays) and morphometric characters (such as placement of the dorsal-fin origin and the dimorphic head width) are discussed. We refer to this phenotypic variant as the mottled-band form of *G. viridis* (Figs. 4, 6).

TABLE 6. Diagnostic and other identifying characters of nominal forms of *Gymnelus viridis*. Boldface type indicates values given as diagnostic; other values are from the descriptions of type and other specimens (Chernova 1998, 1999b, 2000).

Character	<i>G. barsukovi</i> N = 10; 156–243 mm TL	<i>G. platycephalus</i> N = 7; 85–143.5 mm TL	<i>G. gracilis</i> N = 6; 47–87 mm TL	<i>G. obscurus</i> N = 3; 122–156 mm TL	<i>G. bilabrus</i> * N = 9; 53–191 mm TL
Supratemporal commissure	Complete	Complete	Interrupted	Complete	Complete
Coloration	Uniform dark	Mottled	Multi-banded	Uniform dark	Banded-mottled
Predorsal length, % TL	16.3–19.7	15.2–19.5	16.4–18.9	15.2–16.6	17.0–20.0
Head width, % HL	50.0–64.0	44.0–65.0	41.0–50.0	39.0–56.0	44.0–59.0
Head depth, % HL	44.0–58.0	43.0–47.0	40.0–45.0	46.0–50.3	43.0–52.0
Head length, % TL	14.5–17.6	13.8–16.0	12.8–14.9	14.7–15.5	15.0–17.0
Eye diameter, % HL	14.4–21.4	19.4–25.8	17.9–31.0	14.6–22.3	16.0–21.0
Gill slit L, % HL	21.2–28.9	18.4–26.1	21.0–23.3	28.5–30.0	Not given
Pectoral fin L, % HL	49.0–56.0	47.0–55.0	54.0–55.0	46.0–57.0	53.0–59.0
Upper jaw L, % HL	40.0–54.0	39.0–48.0	39.0–44.0	42.0–51.0	43.0–53.0
Body depth at A-fin origin, % TL	7.2–10.2	6.0–8.7	5.1–6.4	6.6–9.5	7.6–9.0
Interorbital width	Almost = eye	Almost = eye	Not given	Male = 1.5 times eye Female = eye diameter	< eye
Free dorsal fin	0–1	0–1	2	0	0–1
pterygiophores					
Vertebrae	95–101	94–101	94–98	94–96	93–99
Maximum L, mm TL	243	143.5	“slightly” > 82 “Thin”	156	191
Body form	Cylindrical	Compressed		Male = cylindrical Female = compressed	Cylindrical

*Head pores with variation in suborbitals were given as diagnostic (Chernova 1998). As these are typical of all *Gymnelus* species, they are not repeated here. The diagnosis includes the holotype and eight non-types.

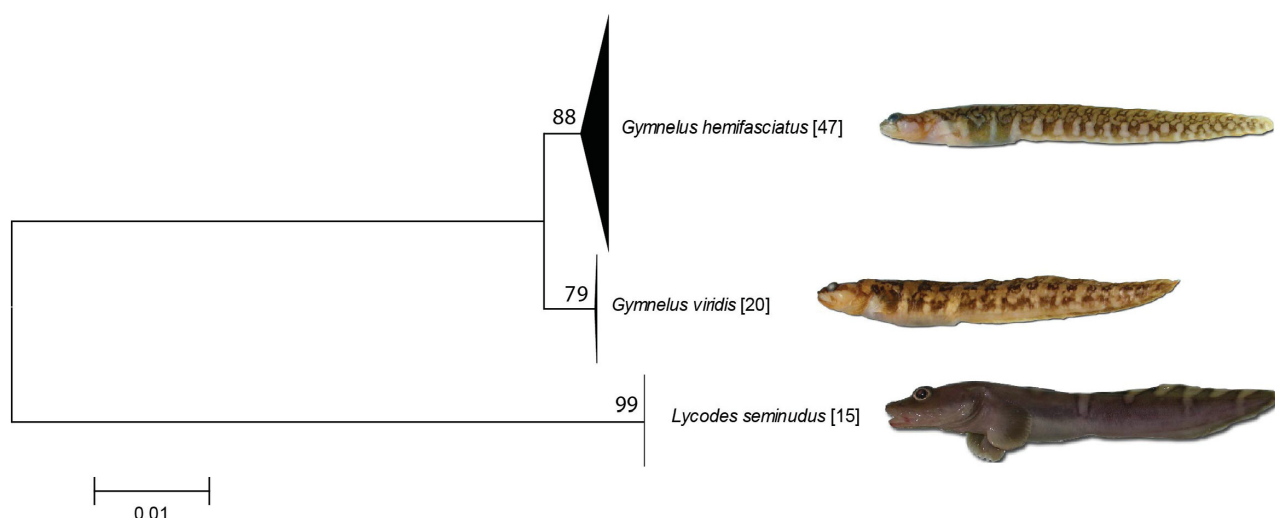


FIGURE 7. Summary neighbor-joining tree of COI sequence divergences between *Gymnelus hemifasciatus*, *G. viridis*, and another zoarcid, *Lycodes seminudus*. The *Gymnelus* samples include specimens from the Bering, East Siberian, Chukchi, and Beaufort seas. The *L. seminudus* sample includes material from the Greenland Sea and Baffin Bay as well as the Chukchi and Beaufort seas. Numbers at nodes represent bootstrap values. The number of specimens follows each species name. The scale bar represents K2P distance.

Discussion

About 98% of the species included in the barcode reference library developed for studies of Pacific Arctic marine fishes (Mecklenburg *et al.* 2011) exhibited distinct barcodes, allowing their unambiguous identification. Most species showed little intraspecific variation (adjusted mean = 0.3%), but a few species had multiple lineages showing much more divergence and likely include overlooked species. Such lineages in *Icelus* Krøyer 1845 and *Mallotus* Cuvier 1829 were highlighted (Mecklenburg *et al.* 2011). In contrast, a few other genera or species contained two or more putative species that lacked barcode divergence. Such cases could reflect hybridization, young taxa, or taxonomic over-splitting (Steinke *et al.* 2009b). In the earlier *Gymnelus* sample and the expanded fresh sample the specimens, which would have been identified as various species using Chernova's (1998a, 1999a,b) descriptions, fell into only two groups (*G. hemifasciatus* and *G. viridis*) that lacked in-group divergence, supporting the conclusion that Chernova's nominal forms represent a case of over-splitting. The complete lack of any coherence of specimens within the groups by geography, sex, or coloration disallows identifying the observed morphotypes as young taxa. Although the sequences in the *G. hemifasciatus* clade displayed a relatively high degree of variability, the variability is well within the range reported in prior barcoding studies on fishes (e.g., Steinke *et al.* 2009a; Ward *et al.* 2009). DNA sequences only from the Pacific Arctic were included in the present study and the *G. viridis* sample included only the mottled-band morphotype. The DNA sequences from *G. viridis* in the fresh sample of Pacific Arctic individuals are just ~0.3% different from *G. viridis* taken off southern Greenland and the Gulf of St. Lawrence. In essence, although there is a difference between Pacific Arctic and Atlantic populations it is not enough to indicate they are different species (D. Steinke, Biodiversity Institute of Ontario, pers. comm. 2014).

Identifications made by experts of fish specimens which are nevertheless not compliant with barcoding expectations has been pointed to as the most difficult type of problem in assessing barcoding results (e.g., McCusker *et al.* 2012). Identifications of *Gymnelus* are an example of the problem. The results from COI sequencing of *Gymnelus* reflect the variability and lack of diagnostic strength of characters recently used (Chernova 1998a, 1999a,b, 2000) to describe species of *Gymnelus*. The barcodes do not support a set number of groups within each of the two species. The unreliability of coloration in particular for distinguishing species is further illustrated by the lack of genetic variability in the *Lycodes seminudus* sample at the barcode locus (Fig. 7) despite this species' rather significant variations in coloration. The *L. seminudus* sample includes uniformly white to black specimens from the continental slope off the Chukchi and Beaufort seas and distinctly banded specimens

from the deep fjords of northeastern Greenland and southern Baffin Bay off western Greenland and Baffin Island, Canada. Occurrence of one form is generally not exclusive of the other. Both forms have been taken in most regions (Jensen 1904), including the Pacific Arctic (Mecklenburg, unpubl.).

As we found with *Gymnelus*, Byrkjedal *et al.* (2014) evaluated three nominal species of fathead sculpin (Psychrolutidae: *Cottunculus* Collett 1875) and found that important morphological characters alone combined in a manner that made species identification impossible. Thus, they analyzed presumed diagnostic characters and compared morphological variation with that found in sequences of the COI gene. The sequences showed almost no variation despite the fact that the sequenced material spanned the whole range of character variation. Their analysis would not support recognition of more than one species.

Reviewing the identifications of *Gymnelus* specimens taken by the RUSALCA expeditions is important because of ongoing efforts to synthesize results of the program and because the situation illustrates problems with identifying *Gymnelus* material in the Pacific Arctic. In 2004 the RUSALCA collected 12 specimens of *Gymnelus*. The present authors examined them together a few days after the expedition and identified them as *G. hemifasciatus* and *G. viridis*. Examining them in 2005 and 2006, Chernova identified the *G. hemifasciatus* material as *G. knipowitschi* and *G. platycephalus*, and *G. viridis* as *G. bilabrus*. Reporting on the 2004 catch, the RUSALCA team compromised and referred to them as *Gymnelus* spp. in the text and included the alternate identifications in the captions to the photographs (Mecklenburg *et al.* 2007: fig. 3). Chernova (2009a,b; pers. comm.) identified the additional RUSALCA material from the expeditions in 2009 and 2012 (20 specimens) as *G. platycephalus* and *G. knipowitschi* and has relegated the one *G. viridis* caught in 2004 and another in 2012 to the status of “unidentified.” The RUSALCA material identified as *G. platycephalus* by Chernova does not match the description (Chernova 1999b) of that nominal species, which, as we have shown, is a junior synonym of *G. viridis*. The specimens identified by Chernova in the recent sample as *G. platycephalus* are, according to our morphological analysis, examples of the typical form of *G. hemifasciatus*. None of the specimens taken by the nets on Pacific Arctic scientific cruises could be identified as *G. platycephalus* from the published description (Chernova 2000). Thus, Chernova’s identifications conflict with her published descriptions. This has led to confusion among biologists identifying material from the RUSALCA and other Pacific Arctic surveys, as exemplified by the mistaken conclusion (Mecklenburg *et al.* 2011) that *G. platycephalus* is a synonym of *G. hemifasciatus* when it actually is a synonym of *G. viridis*.

The entire omission of *G. viridis* or one of its junior synonyms, such as *G. bilabrus* or *G. barsukovi*, from recent lists of Chukchi Sea fish species (Chernova 2009a,b; pers. comm.) is incomprehensible. The one specimen of *G. viridis* identified earlier by Chernova as *G. bilabrus* and later demoted to unidentified status is actually a good example of the *bilabrus* morphotype (see Mecklenburg *et al.* 2007: fig. 3). In fact, more than half the barcoded *G. viridis* specimens from our fresh sample (Fig. 1) are the *bilabrus* color morph of *G. viridis*, and most were taken in the Chukchi Sea. Moreover, Andriashev (1937) described *G. bilabrus* from Bering Strait material and reported (Andriashev 1952, 1954) *G. viridis* to be common in the Chukchi Sea.

The extreme rarity of catching the two morphotypes of *G. hemifasciatus* together suggests some ecological difference. Chernova (2000:8) suggested ecological differences among her new nominal species by stating that “*G. knipowitschi* prefers negative water temperatures and inhabits shallow areas up to 100 m (rarely to 175 m),” whereas “*G. diporus* was found under positive temperatures at depths from 123 to 200 m.” This difference could not be substantiated by only two specimens of *G. diporus* on which the description was based, and by bottom depths only to 100 m present in our Pacific Arctic sampling area. Besides, ecological differences recorded for collected specimens do not equate to validation of the presence of different species.

Anderson & Fedorov (2004) suggested that some of the new nominal species of *Gymnelus* could be ecophenotypes of the previously described species, and there are strong indications of differences in the substrates, depths, and temperatures at which the *G. hemifasciatus* morphotypes in the fresh sample were taken. Both morphotypes of *G. hemifasciatus* were taken in a wide range of temperatures (−1.5° to 10.5°C, typical morphotype; −1.8° to 6.9°C, solid-band morphotype [Table 4]), but the solid-band morphotype, which was most similar to the nominal form *G. knipowitschi*, was taken more often at negative temperatures (48% of stations where it was caught) than the typical morphotype (14%). It also often occurred at depths greater than 60 m (22% of stations where it was caught) whereas the typical form, except for one specimen, always occurred at depths of 60 m or less (94% of stations where caught). Observations of the substrate in net contents indicated that the typical morphotype of *G. hemifasciatus* was more often associated with harder and rougher substrate, including more gravel, shell hash,

cobble, and boulders, compared with the solid-band morphotype. The same impression was gained from plotting the catch localities on a map of the sediments in the region (Fig. 5), where it was seen that the solid-band morphotype of *G. hemifasciatus* occurred mostly on substrate with a high proportion of mud, including all mud or sandy mud with no gravel, whereas the typical or classic morphotype was found on sediments comprising all gravel or with a high proportion of gravel.

The discussion by Mallet (2008) of mosaic sympatry and maintenance of “ecotypes” (or ecophenotypes) in different habitats by their close proximity and opportunity for maintaining genetic continuity may have particular bearing for *Gymnelus* populations. Mosaic sympatry could explain the many variations within each species or morphotype. The morphotypes are regionally sympatric but are associated with different habitats within the regions. Many examples of such ecologically differentiated forms exist in nature; for instance, among fishes, freshwater and marine forms in sticklebacks (*Gasterosteus aculeatus* Linnaeus 1758) with differences in body armor (Bell & Foster 1994) and adaptations to presence or absence of predators in guppies (*Poecilia reticulata* Peters 1859) reflected in head morphology and size at maturity (Torres-Dowdall *et al.* 2012). *Gymnelus* phenotypes may be another example. If corresponding genetic differences have arisen they are not detectable at the barcode locus.

To gain further understanding of the morphotypes within *Gymnelus* species it will be necessary to analyze catches for which environmental variables can be reliably quantified, rather than having to rely on voucher specimens which may not reflect actual numbers and proportions of species caught and which often have little environmental information associated with them. Moreover, the sparse ecological data that have been published may not always be accurate. For instance, although data were reported for *G. viridis* taken from the Beaufort and Chukchi seas by bottom trawl in 1977 (Frost & Lowry 1983), examination of voucher specimens from 6 of the 12 stations at which *G. viridis* was reported to have been caught revealed they were misidentified *G. hemifasciatus* (Mecklenburg, unpubl.).

Several errors, exclusions, or misinterpretations among the new Russian papers require addressing here. Chernova (1998a) basically diagnosed *Gymnelus viridis* (17 specimens from eastern Canada and southwestern Greenland) as a form with relatively high vertebral counts (97–104), an interrupted supratemporal commissure, a relatively deep pectoral-fin base and other overlapping morphometric characters, and a monotonous coloration. Of the 59 monotone specimens studied by Anderson (1982) and our 2014 visit to the California Academy of Sciences, and identified as *G. viridis*, 22 (37.3%) possessed an incomplete supratemporal commissure with two occipital pores and 37 (62.7%) had complete commissures with three occipital pores (= *G. “barsukovi”* or *G. “obscurus”* morphotypes depending on ontogenetic head and eye morphometry). Significantly, these morphotypes occurred together in four general localities: (1) southern Greenland (Julianehaab, Lindenowfjord); (2) eastern Arctic Canada off southern Baffin Island; (3) central Arctic Canada at Resolute, Cornwallis Island; and (4) the Beaufort Sea at Liverpool Bay, Canada. Two collections at Liverpool Bay (NMC 77-1259 and 77-1260) contained two monotone specimens each with a complete supratemporal commissure with three occipital pores, and one each with an incomplete commissure with two occipital pores. At Resolute two collections were made with the same conditions: NMC 65-355 is a monotone specimen with an incomplete supratemporal commissure and two occipital pores, and in NMC 62-399 are two monotone specimens with a complete commissure and three occipital pores. Among the material studied by Anderson (1982), Chernova (1998a:167) examined one specimen (ZMUC P76169) that both she and Anderson (1982) identified as *G. viridis* from southern Greenland but that Anderson found to have a complete supratemporal commissure with three occipital pores making it a *G. “barsukovi”* morphotype. Thus it appears that Chernova’s (1998a) understanding of *G. viridis* omitted atypical natural variation owing to her small sample size and so relied on some selectivity. Other atypical conditions of characters were noted by Anderson (1982) and not mentioned by Chernova in her five papers. Of the 291 specimens Anderson (1982) examined of *G. viridis*, 6 (97–192 mm SL) lacked palatine teeth. They were from the Bering and Beaufort seas and central Arctic Canada. The interorbital pore was found in eight specimens of *G. viridis* (not seven as given by Anderson [1982:30]) from central and eastern Arctic Canada. Those two characters were accepted by Chernova (2000) in retaining the nominal genus *Commandorella* Taranetz & Andriashev, 1935, which we reject. Absence of palatal teeth (either vomerine or palatine or both) is also characteristic of *Lycodes cortezianus* (Gilbert 1890), *L. pacificus* Collett 1879, and five species of *Lycenchelys* (Anderson 1994, 1995, 2006). Variation in other head pore counts in *G. viridis* is found in Anderson (1982:32). Data on branchiostegal ray condition was recorded for 204 of the 291 specimens. Ray number was usually six on each side (6 + 6), but one specimen was found with formula 5 + 6 and

two had 7 + 7. Branchiostegal ray data were taken on 78 of the 113 specimens of *G. hemifasciatus*. The typical formula 6 + 6 was found in 64 fish, and one had formula 6 + 7, five had 5 + 6, and eight had 5 + 5.

In her synonymy of *Gymnelus barsukovi* Chernova (1999b:347) erroneously listed five ZIN lots (14146, 25332, 34984, 34988, and 35423) studied by Anderson (1982) as well, to *G. hemifasciatus*. These in fact are specimens of *G. viridis* and were so listed by Anderson (1982:73).

Chernova (1999a) identified the specimen named *Nemalycodes grigorjewi* Herzenstein 1896 (ZIN 9688), from the Barents Sea as belonging to a species other than *G. viridis*, originally placed in synonymy with the latter by Knipowitsch (1901, 1908). The specimen is destroyed and unidentifiable, the description is nondiagnostic, there are three *Gymnelus* species in the Barents Sea (Anderson 1982: figs. 20, 25), and it was designated *nomen dubium* (Anderson 1982:56). However, Chernova (1999a:1), employing incorrect taxonomic procedure, placed the senior name *N. grigorjewi* as a synonym of her new nominal form *G. knipowitschi*. Near the end of this paper Chernova (1999a:7) states "... I tentatively consider *N. grigorjewi* as a synonym of the new species; at the same time, I believe that there is no basis yet to reinstate the specific name *grigorjewi*." This confusing taxonomic form appears, on the one hand, to make *G. knipowitschi* automatically a junior synonym of *N. grigorjewi* and, on the other hand, if Chernova does not want to "reinstate" the senior name, it would also appear that she may agree that the status of the name should remain a *nomen dubium*. We would avoid this kind of confusion and regard *N. grigorjewi* as a *nomen dubium* still.

Finally, three other nominal species of *Gymnelus* were described from western Russian Arctic seas and Svalbard: *G. andersoni* (Chernova 1998b) and *G. esipovi* and *G. taeniatus* (Chernova 1999b). As the areas and character evaluation are beyond the scope of this paper, we offer here just a few comments. All nominal forms have a retrograde dorsal-fin origin, thus resembling *G. retrodorsalis* Le Danois 1913, and similar meristics and morphometrics, but head canals and pore variation differ.

Gymnelus andersoni was described from 24 types, with 57 additional specimens listed ranging from the Barents to Laptev seas. It was diagnosed by its discontinuous suborbital (infraorbital) canal with few anterior and posterior pores, in conjunction with the supratemporal commissure "usually lacking" (Chernova 1998b:711). She found 7% of her sample (24 types and 57 others) possessed a partial supratemporal commissure with two lateral pores (pattern 1-0-1). Anderson's (1982) data concur and the second author's re-examination of his data found two lots (ZIN 14138: 5; 102–119 mm SL; and ZIN 14155: 2; 122, 124 mm SL) with both the *G. andersoni* and typical *G. retrodorsalis* morphotypes from the same trawl haul. Chernova (1998b:714) listed only those specimens that fit her *G. retrodorsalis* diagnosis in that species' redescription and did not list the others which fit her *G. andersoni*. This again questions the diagnostic strength of the completeness of the supratemporal commissure (see above) and its variable pore distributions.

Gymnelus esipovi was described from nine types with four others listed ranging from Svalbard to the Kara Sea (Chernova 1999b). It was diagnosed by its discontinuous supratemporal commissure and its "comparatively high number of vertebrae," as well as the retrograde dorsal-fin origin and other characters we consider here (as with *G. hemifasciatus* and *G. viridis* above) as nondiagnostic: cylindrical body, large eye, numerous teeth, and small size. Vertebral counts for the type series are 98 (holotype) and 96–100 (paratypes) (Chernova 1999b:343). The second author's re-examination of his original (1982) data give vertebrae 95 (holotype) and 95–101 (paratypes) for seven specimens in three lots: ZIN 30558, ZIN 14139, and ZIN 29453. Comparing Chernova's nine specimens with Anderson's (1982) data on other *Gymnelus* specimens with the retrograde dorsal-fin origin and the incomplete supratemporal commissure, we find the vertebral count not especially "high" (see Anderson 1982: fig. 23). Thus, we consider *G. esipovi* a junior synonym of *G. retrodorsalis* Le Danois 1913. Further, the female paratype, 104 mm SL (106.5 mm TL) in ZIN 29453, has five occipital pores emanating from the supratemporal commissure instead of the usual two lateral ones, again diminishing the diagnostic strength of this feature.

Gymnelus taeniatus was described from a single juvenile female from Franz Josef Land (Chernova 1999b). It was diagnosed by its incomplete supratemporal commissure and six features we deem nondiagnostic. Because of its recent capture (collected 7 years before its description), especially of concern are the "high head and body" and very evident lateral line, conditions we know to significantly alter with time in preservative. Lacking additional comparative material from the area, this form appears to be a *G. retrodorsalis* with few (five) free dorsal pterygiophores (interneurons), not remarkable in other specimens from western Arctic Russia seen by Anderson (1982).

Acknowledgments

Support for the first author for this project was provided by the U.S. National Oceanic and Atmospheric Administration (NOAA), Arctic Research Program, for the Russian–American Long-Term Census of the Arctic (RUSALCA). Support for the second author was provided by the South African Institute of Aquatic Biodiversity of the National Research Foundation, Pretoria, South Africa. Dirk Steinke, Biodiversity Institute of Ontario, University of Guelph, Canada provided the analysis of the DNA sequences, created Figs. 1 and 7, and reviewed the manuscript. Kathleen Crane, NOAA, Arctic Research, Bethesda, Maryland provided the sediment shapefiles for Fig. 5. Brenda A. Holladay, University of Alaska Fairbanks, provided salinity and temperature data from Pacific Arctic expeditions. We are grateful to the curators and collection managers for their care of the material, providing space during visits, and loaning specimens when we could not be there: William N. Eschmeyer, Tomio Iwamoto, David Catania, Jon Fong, Mysi Hoang, California Academy of Sciences; and J. Andres Lopez, University of Alaska Museum of the North. We thank an anonymous reviewer, Gento Shinohara, and Eric Hilton for helpful suggestions during the review process.

References

- Anderson, M.E. (1982) Revision of the fish genera *Gymnelus* Reinhardt and *Gymnelopsis* Soldatov (Zoarcidae), with two new species and comparative osteology of *Gymnelus viridis*. *National Museums of Canada (Ottawa) Publications in Zoology*, 17, 1–76.
- Anderson, M.E. (1988) Studies on the Zoarcidae (Teleostei: Perciformes) of the southern hemisphere. I. The Antarctic and subantarctic regions. *Antarctic Research Series*, 47, 59–113.
<http://dx.doi.org/10.1029/AR047p0059>
- Anderson, M.E. (1989) Review of the eelpout genus *Pachycara* Zugmayer, 1911 (Teleostei: Zoarcidae), with descriptions of six new species. *Proceedings of the California Academy of Sciences*, 46 (10), 221–242.
- Anderson, M.E. (1994) Systematics and osteology of the Zoarcidae (Teleostei: Perciformes). *Ichthyological Bulletin, J. L. B. Smith Institute of Ichthyology*, 60, 1–120.
- Anderson, M.E. (1995) The eelpout genera *Lycenchelys* Gill and *Taranetzella* Andriashev (Teleostei: Zoarcidae) in the eastern Pacific, with descriptions of nine new species. *Proceedings of the California Academy of Sciences*, 49 (2), 55–113.
- Anderson, M.E. (2006) Studies on the Zoarcidae (Teleostei: Perciformes) of the southern hemisphere. XII. Two new lycodine species from off Peru. *Species Diversity*, 11 (3), 183–190.
- Anderson, M.E. & Fedorov, V.V. (2004) Family Zoarcidae Swainson 1839 — eelpouts. *California Academy of Sciences Annotated Checklists of Fishes*, 34, 1–58.
- Anderson, M.E., Stevenson, D.E. & Shinohara, G. (2009) Systematic review of the genus *Bothrocara* Bean 1890 (Teleostei: Zoarcidae). *Ichthyological Research*, 56 (2), 172–194.
<http://dx.doi.org/10.1007/s10228-008-0086-6>
- Andriashev, A.P. (1937) A contribution to the knowledge of the fishes from the Bering and Chukchi seas. *Issled Morei SSSR 25 (Issled Dal'nevostoch Morei 5)*, 292–355, figs. 1–27. [Leningrad. Lanz L. & Wilimovsky N.J. (translators) 1955, *U.S. Fish and Wildlife Service Special Scientific Report—Fisheries*, 145, 81 pp.]
- Andriashev, A.P. (1952) Fishes of the Chukchi Sea and Bering Strait. *Krayniy Severo-Vostok Soyuza SSR. Vol. 2. Fauna i Flora Chukotskogo Morya*, 311–322. [Moscow, Akademii Nauk SSSR, in Russian.]
- Andriashev, A.P. (1954) *Fishes of the northern seas of the U.S.S.R. Opredeliteli po Faune SSSR*, 53. Akademii Nauk SSSR, Moscow, 567 pp. [in Russian; and English translation, 1964, Israel Program for Scientific Translations, 617 pp.]
- Balanov, A.A. & Kukhlevskii, A.D. (2011) Variation of coloration in *Lycodes yamatoi* Toyoshima, 1985 (Pisces: Zoarcidae) in the northern Sea of Japan. *Russian Journal of Marine Biology*, 37 (6), 464–471.
<http://dx.doi.org/10.1134/s1063074011060046>
- Balushkin, A.V., Sheiko, B.A. & Fedorov, V.V. (2011) Catalog of archival collection of the Zoological Institute, Russian Academy of Sciences: Class Osteichthyes (bony fishes), order Perciformes, family Zoarcidae. *Journal of Ichthyology*, 51, 950–1034.
<http://dx.doi.org/10.1134/S0032945211100031>
- Bean, T.H. (1890) Scientific results of explorations by the U. S. Fish Commission steamer Albatross. No. XI. New fishes collected off the coast of Alaska and the adjacent region southward. *Proceedings of the United States National Museum*, 13, 37–45.
<http://dx.doi.org/10.5479/si.00963801.13-795.37>
- Bell, M.A. & Foster, S.A. (1994) *The Evolutionary Biology of the Threespine Stickleback*. Oxford University Press, Oxford, 571 pp.
- Byrkjedal, I., Hadler-Jacobsen, S., Rees, D. & Orlov, A. (2014) Molecular and morphological variation in saddled fathead

- sculpins (Psychrolutidae: *Cottunculus*) of the north-east Atlantic Ocean, with a synonymy of three species. *Journal of Fish Biology*, 85 (3), 821–837.
<http://dx.doi.org/10.1111/jfb.12458>
- Chernova, N.V. (1998a) Reestablishment of the validity of species *Gymnelus bilabrus* Andriashev 1937 with characteristics of species *G. viridis* verified (Fabricius, 1780) (Zoarcidae). *Journal of Ichthyology*, 38, 163–169. [Russian in *Voprosy Ikhtiologii*, 38, 182–188.]
- Chernova, N.V. (1998b) A new species *Gymnelus andersoni* sp. nova, from the Arctic seas with refinement of the species status of *G. retrodorsalis* Le Danois and *G. pauciporus* Anderson (Fam. Zoarcidae). *Journal of Ichthyology*, 38, 708–715. [Russian in *Voprosy Ikhtiologii*, 38, 737–744.]
- Chernova, N.V. (1999a) New species *Gymnelus knipowitschi* from the Arctic Ocean and a redescription of *G. hemifasciatus* Andriashev (Zoarcidae). *Journal of Ichthyology*, 39, 1–9. [Russian in *Voprosy Ikhtiologii*, 39, 5–13.]
- Chernova, N.V. (1999b) Four new species of *Gymnelus* (Zoarcidae) from the Arctic regions. *Journal of Ichthyology*, 39, 343–352. [Russian in *Voprosy Ikhtiologii*, 39, 306–315.]
- Chernova, N.V. (2000) Four new species of *Gymnelus* (Zoarcidae) from the Far Eastern seas with genus diagnosis and key to species. *Journal of Ichthyology*, 40, 1–12. [Russian in *Voprosy Ikhtiologii*, 40, 5–16.]
- Chernova, N.V. (2009a) Review of fish fauna of the Chukchi Sea. In: *13th European Congress of Ichthyology, 6–12 September*. Klaipeda, Lithuania, pp. 19.
- Chernova, N.V. (2009b) Review of fish fauna of the Chukchi Sea. In: *Modern Problems of Theoretical and Practical Ichthyology, September 16–19, 2009. Abstracts*. Sevastopol, Ukraine, pp. 173–175. [in Russian]
- Collett, R. (1875) *Norges fiske, med bemaerkninger om deres Udberedelse*. Christiania, A.W. Brøgger, 240 pp.
<http://dx.doi.org/10.5962/bhl.title.14429>
- Collett, R. (1879) Fiske fra Nordhavs-Expeditionens sidste Togt, Sommeren 1878. *Forhandlinger i Videnskabs-selskabet i Christiania*, 14, 1–106.
- Collett, R. (1879) On a new fish of the genus *Lycodes* from the Pacific. *Proceedings of the Zoological Society of London 1879*, 2 (4), 381–382.
<http://dx.doi.org/10.1111/j.1096-3642.1879.tb02667.x>
- Cuvier, G. (1829) *Le Règne Animal, distribué d'après son organisation, pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie compare*. Vol. 2. 2nd Edition. Chez Déterville, Paris, 305 pp.
- Fabricius, O. (1780) Fauna groenlandica, systematice sistens animalia Groenlandiae occidentalis hactenus indagata, quoad nomen specificum, trivale, vernaculumque. I. G. Rothe, Hafniae & Lipsiae (Copenhagen & Leipzig), i–xvi + 1–452, 1 pl.
- Frost, K.J. & Lowry, L.F. (1983) *Demersal fishes and invertebrates trawled in the northeastern Chukchi and western Beaufort seas, 1976–77*. U.S. Department of Commerce, NOAA Technical Report NMFS SSRF-764, 22 pp.
- Garman, S. (1899) The Fishes. In: Reports on an exploration off the west coasts of Mexico, Central and South America, and off the Galapagos Islands, in charge of Alexander Agassiz, by the U. S. Fish Commission steamer “Albatross” during 1891, Lieut.-Commander Z.L. Tanner, U.S.N., commanding. No. XXVI. *Memoirs of the Museum of Comparative Zoology*, 24, 1–431.
- Gilbert, C.H. (1890) A preliminary report on the fishes collected by the steamer Albatross on the Pacific coast of North America during the year 1889, with descriptions of twelve new genera and ninety-two new species. *Proceedings of the United States National Museum*, 13, 49–126.
<http://dx.doi.org/10.5479/si.00963801.13-797.49>
- Goode, G.B. & Bean, T.H. (1896) Oceanic ichthyology, a treatise on the deep-sea and pelagic fishes of the world, based chiefly upon the collections made by the steamers Blake, Albatross, and Fish Hawk in the northwestern Atlantic, with an atlas containing 417 figures. *Smithsonian Contributions to Knowledge*, 30 & 31, 1–553 & pls. 1–123.
- Green, J.M. & Mitchell, L.R. (1997) Biology of the fish doctor, an eelpout, from Cornwallis Island, Northwest Territories, Canada. *American Fisheries Society Symposium*, 19, 140–147.
- Herzenstein, S. (1896) Über einige neue und seltene Fische des Zoologischen Museums der Kaiserlichen Akademie der Wissenschaften. *Ezhagodnik. Zoologicheskogo Muzeya Imperatorskoj Akademii Nauk*, 1 (1), 1–14.
- Jensen, A.S. (1904) The North-European and Greenland Lycodinae. *The Danish Ingolf-Expedition*, 2 (4), 1–99, 10 pls.
- Jensen, A.S. (1952) Recent finds of Lycodinae in Greenland waters. *Meddelelser om Grønland*, 142 (7), 1–28.
- Jordan, D.S. & Hubbs, C.L. (1925) Record of fishes obtained by David Starr Jordan in Japan, 1922. *Memoirs of the Carnegie Museum*, 10, 93–346.
- Kimura, M. (1980) A simple method for estimating evolutionary rates of base substitutions through comparative studies of nucleotide sequences. *Journal of Molecular Evolution*, 16, 111–120.
<http://dx.doi.org/10.1007/BF01731581>
- Knipowitsch, N.M. (1901) Zoologische Ergebnisse der Russischen Expeditionen nach Spitzbergen. Ueber die in den Jahren 1899–1900 im Gebiete von Spitzbergen gesammelten Fische. *Annals of the Museum of Zoology, Imperial Academy of Sciences, St. Petersburg*, 6, 56–83.
- Knipowitsch, N.M. (1906) Ichthyologische Untersuchungen im Eismeer. I. *Lycodes* und *Lycenchelys*. *Mémoires de l'Académie Impériale des Sciences de St. Petersbourg*, 19 (1), 1–130.
- Knipowitsch, N.M. (1908) Ichthyologische Untersuchungen im Eismeer. I. *Gymnelus* und *Enchelyopus*. *Mémoires de l'Académie Impériale des Sciences de St. Petersbourg, Series 8*, 22 (4), 1–40.

- Krøyer, H.N. (1845) Ichthyologiske Bidrag. *Naturhistorisk Tidsskrift (Kjøbenhavn)*, 1, 253.
- Le Danois, E. (1913) Études sur quelques poissons des océans Arctique et Atlantique. *Annales de l'Institut Océanographique Monaco*, 7 (2), 1–75.
- Linnaeus, C. (1758) *Systema Naturae*, 10th edition. Vol. 1. (*Systema naturae per regna tria naturae, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata.*) Holmiae, 295 pp.
- Mallet, J. (2008) Hybridization, ecological races and the nature of species: empirical evidence for the ease of speciation. *Philosophical Transactions of the Royal Society B*, 363, 2971–2986.
<http://dx.doi.org/10.1098/rstb.2008.0081>
- McAllister, D.E., Anderson, M.E. & Hunter, J.G. (1981) Deep-water eelpouts, Zoarcidae, from Arctic Canada and Alaska. *Canadian Journal of Fisheries and Aquatic Sciences*, 38, 821–839.
<http://dx.doi.org/10.1139/f81-110>
- McCusker, M.R., Denti, D., Van Guelpen, L., Kenchington, E. & Bentzen, P. (2012) Barcoding Atlantic Canada's commonly encountered marine fishes. *Molecular Ecology Resources*, 13, 177–188.
<http://dx.doi.org/10.1111/1755-0998.12043>
- Mecklenburg, C.W., Mecklenburg, T.A. & Thorsteinson, L.K. (2002) *Fishes of Alaska*. American Fisheries Society, Bethesda, xxxvii + 1037 pp.
- Mecklenburg, C.W., Möller, P.R. & Steinke, D. (2011) Biodiversity of arctic marine fishes: taxonomy and zoogeography. *Marine Biodiversity*, 41, 109–140 + Online Resources 1–5.
<http://dx.doi.org/10.1007/s12526-010-0070-z>
- Mecklenburg, C.W., Stein, D.L., Sheiko, B.A., Chernova, N.V., Mecklenburg, T.A. & Holladay, B.A. (2007) Russian–American Long-term Census of the Arctic: benthic fishes trawled in the Chukchi Sea and Bering Strait, August 2004. *Northwestern Naturalist*, 88, 168–187.
[http://dx.doi.org/10.1898/1051-1733\(2007\)88\[168:RLCOTA\]2.0.CO;2](http://dx.doi.org/10.1898/1051-1733(2007)88[168:RLCOTA]2.0.CO;2)
- Møller, P.R. (2000) Restoration of the taxon *Lycodes marisalbi*, with notes on its disjunct Arctic distribution. *Journal of Fish Biology*, 57, 1404–1415.
<http://dx.doi.org/10.1111/j.1095-8649.2000.tb02220.x>
- Møller, P.R. (2001) Redescription of the *Lycodes pallidus* species complex (Pisces, Zoarcidae), with a new species from the Arctic/North Atlantic Ocean. *Copeia*, 2001, 972–996.
[http://dx.doi.org/10.1643/0045-8511\(2001\)001\[0972:ROTLPS\]2.0.CO;2](http://dx.doi.org/10.1643/0045-8511(2001)001[0972:ROTLPS]2.0.CO;2)
- Møller, P.R. & Jørgensen, O.A. (2000) Distribution and abundance of eelpouts (Pisces, Zoarcidae) off west Greenland. *Sarsia*, 85, 23–48.
- Okiyama, M. (2004) Deepest demersal fish community in the Sea of Japan: a review. *Contributions of the Biological Laboratory, Kyoto University*, 29, 409–429.
<http://hdl.handle.net/2433/156411>
- Peters, W.(C.H.) (1859) Eine neue vom Herrn Jagor im atlantischen Meere gefangene Art der Gattung *Leptocephalus*, und über einige andere neue Fische des Zoologischen Museums. *Monatsberichte der Königlich Preuss[ischen] Akademie der Wissenschaften zu Berlin*, 1859, 411–413.
- Ratnasingham, S. & Hebert, P.D.N. (2007) The Barcode of Life Database. *Molecular Ecology Notes*, 7, 355–364.
<http://dx.doi.org/10.1111/j.1471-8286.2007.01678.x>
- Reinhardt, J.C.H. (1831) Bidrag til vor Kundskab om Grönlands Fiske. In: H.C. Örsted. *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger og dets Medlemmers Arbejder (Kjøbenhavn)*, 1830–31, 18–24.
- Reinhardt, J.C.H. (1834) Om *Gymnelus*. In: H.C. Örsted. *Oversigt over det Kongelige Danske Videnskabernes Selskabs Forhandlinger og dets Medlemmers Arbejder (Kjøbenhavn)*, 1831–32, 4.
- Saveliev, P.A., Balanov, A.A. & Kukhlevskii, A.D. (2014) On the colour types in *Lycodes nakamurae* (Tanaka, 1914) and species composition of the subgenus *Furcimanus* (Perciformes: Zoarcidae: *Lycodes*) in the Sea of Japan. *Zootaxa*, 3811 (1), 119–128.
<http://dx.doi.org/10.11646/zootaxa.3811.1.7>
- Shinohara, G., Nazarkin, M.V. & Chereshevnev, I.A. (2004) *Magadania skopetsi*, a new genus and species of Zoarcidae (Teleostei: Perciformes) from the Sea of Okhotsk. *Ichthyological Research*, 51 (2), 137–145.
<http://dx.doi.org/10.1007/s10228-004-0209-7>
- Steinke, D., Zemlak, T.S., Boutillier, J.A. & Hebert P.D.N. (2009a) DNA barcoding Pacific Canada's fishes. *Marine Biology*, 156, 2641–2647.
<http://dx.doi.org/10.1007/s00227-009-1284-0>
- Steinke, D., Zemlak, T.S. & Hebert, P.D.N. (2009b) Barcoding Nemo: DNA-based identifications for the ornamental fish trade. *PLoS ONE*, 4 (7), e6300.
<http://dx.doi.org/10.1371/journal.pone.0006300>
- Tamura, K., Peterson, D., Peterson, N., Stecher, G., Nei, M. & Kumar, S. (2011) MEGA5: Molecular evolutionary genetics analysis using maximum likelihood, evolutionary distance, and maximum parsimony methods. *Molecular Biology and Evolution*, 28, 2731–2739.
<http://dx.doi.org/10.1093/molbev/msr121>
- Tanaka, S. (1914) *Furcimanus nakamurae* Tanaka. *Figures and descriptions of the fishes of Japan including Riukiu Islands*,

- Bonin Islands, Formosa, Kurile Islands, Korea and southern Sakhalin*, 18, 303. [in Japanese and English.]
- Taranetz, A.Ya. & Andriashev, A.P. (1935) Vier neue Fischarten der Gattung *Lycodes* Reinh. aus dem Ochotskischen Meer. *Zoologischer Anzeiger*, 112 (9–10), 242–253.
- Torres-Dowdall, J., Handelsman, C.A., Reznick, D.N. & Ghalambor, C.K. (2012) Local adaptation and the evolution of phenotypic plasticity in Trinidadian guppies (*Poecilia reticulata*). *Evolution*, 66 (11), 3432–3443.
<http://dx.doi.org/10.1111/j.1558-5646.2012.01694.x>
- Toyoshima, M. (1985) Taxonomy of the subfamily Lycodinae (family Zoarcidae) in Japan and adjacent waters. *Memoirs of the Faculty of Fisheries Hokkaido University*, 32, (2), 131–243.
- U.S. Department of Commerce, NOAA (National Oceanic and Atmospheric Administration). (1987) *Bering, Chukchi, and Beaufort seas: Coastal and Ocean Zones Strategic Assessment: Data Atlas*. NOAA, Ocean Assessments Division, Rockville, Maryland, 135 pp.
- Ward, R.D., Hanner, R. & Hebert, P.D.N. (2009) The campaign to DNA barcode all fishes, FISH-BOL. *Journal of Fish Biology*, 74, 329–356.
<http://dx.doi.org/10.1111/j.1095-8649.2008.02080.x>